THE ECOLOGY OF A HIGH-LATITUDE ROCKY INTERTIDAL COMMUNITY: PROCESSES DRIVING POPULATION DYNAMICS IN KACHEMAK BAY, ALASKA

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A

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ABSTRACT

The population dynamics and interactions of selected key species relative to community structure were investigated in the rocky intertidal of Kachemak Bay, southcentral Alaska (59°35'N, 151°30'W). The roles of recruitment processes and predation in regulating intertidal populations were emphasized in this investigation.

Species abundances, as indicated by coverage of space, were distinctly seasonal. Total cover typically exceeded 80% during the summer, especially in lower intertidal. Winter cover averaged 40-60%, with macroalgal cover varying up to six-fold between summer and winter.

Barnacle recruitment varied both inter-annually and with respect to species. From 1991-1993, mean recruitment densities varied from 0.85-8.71 cm^{-2} (range= 0-71 cm^{-2}). In the upper intertidal, time-integrated summer recruit density of *Semibalanus balanoides* and *Balanus glandula* was 0.13 cm^{-2}. Recruit density of *S. cariosus* in the low intertidal was 4.32 cm^{-2}. In the low intertidal, recruits often saturated the surface, resulting in density-dependent mortality in two out of three years, a phenomenon which did not occur in the upper intertidal where space was never limiting.

Predation was a significant source of mortality for barnacle recruits only in 1991, a poor recruitment year. However, predation by *Nucella lima* limited mussel (*Mytilus trossulus*) populations at some sites. Where *N. lima* density

exceeded 100 m^{-2}, mussel cover was less than half that where *Nucella* was rare (31% vs. 72%). High densities of *N. lima* were estimated to remove 60-90% of mussels per season.

Recruitment of the macroalga *Fucus gardneri* was almost 50 times greater in the presence of live barnacles than on bare rock surfaces or barnacle shells killed by heating. Recruitment in quadrats with tests of mechanically killed barnacles was intermediate. The results indicate that *F. gardneri* propagules are stimulated to attach by a chemical cue, probably a polypeptide, produced by the barnacles.

Based on population dynamics and species interactions investigated in Kachemak Bay, the mid- to upper intertidal community at high latitudes is structured by recruitment processes. The mid- to low intertidal community appears to function similarly to the classical paradigm of regulation by competition and predation. The major exception is high inter-annual variability in predation relative to recruitment and competition.

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PREFACE

The chapters that compose this dissertation have been written to be submitted separately for publication in refereed scientific journals. Therefore, some repetition occurs between chapters, especially with background information or field methods. This approach is the most efficient means of making the dissertation results available to the scientific community.

ACKNOWLEDGMENTS

Although this work is the creative product of one person, it would have been impossible to complete without the assistance and support of many people. I owe a particular debt of gratitude to my thesis advisor, Ray Highsmith, whose guidance has been seminal, not only to this project, but also to the development of my scientific perspective. I also wish to acknowledge members of my advisory committee (Ted Cooney, Peter McRoy, P.X. Quang, and Don Schell) for their commitment of time and their dissemination of scientific ideas. P.X. Quang was a particularly valuable resource, as his unique ability to bridge the seemingly vast gap between the mystery of pure statistical theory and the valuable tools of applied statistical methods was matched only by his gracious and selfless accessibility to students.

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CHAPTER 1: INTRODUCTION

Research conducted in temperate rocky intertidal communities has contributed greatly to the conceptual and empirical foundations of community ecology (Roughgarden *et al.*, 1988; Grosberg & Levitan, 1992). Field research on species interactions in the 1960's and 1970's resulted in broad generalizations regarding the development and maintenance of intertidal community structure.

The principal paradigm resulting from this large body of early research revolved around the concept of space as a limiting resource in rocky intertidal zones. Species were ranked with respect to their ability to utilize space by overgrowing one another, and competition between species was considered hierarchical. Competition, if left unchecked, would culminate in a monoculture of the dominant organism. The competitive hierarchy however, was often modified by predation. Intense predation on the competitive dominant often prevented exclusion of inferior competitors, resulting in coexistence and increased species diversity. Thus, the competitive hierarchy, together with predation, species tolerances to aerial exposure, and physical disturbance (in the form of wave action) were the primary forces governing patterns of species distribution and abundance. These deterministic processes explained much of the structure of intertidal communities where the early work was conducted (e.g., Connell, 1961, 1970,

Paine, 1966, 1974, 1984; Dayton, 1971; Menge, 1976; Menge & Sutherland, 1976; reviews in Connell, 1972, 1975; Sih *et al.*, 1985).

Most early studies focused on interactions between adults. At geographic locations where extensive intertidal research was conducted, recruitment to the rocky intertidal shore was consistently high (e.g. Connell, 1970). Because space in the intertidal was saturated with recruits each year, the "starting condition" was always similar, and patterns of community structure were consistently determined by post-recruitment processes such as competition and predation. Therefore, no importance was ascribed to recruitment dynamics in determining rocky intertidal community structure.

In the mid-1980's, however, field studies from a variety of intertidal habitats in different geographic regions indicated that consistent, ample recruitment of intertidal species to rocky shores was not universal (Underwood *et al.*, 1983; Underwood & Denly, 1984; Gaines & Roughgarden, 1985; Gaines *et al.*, 1985). These studies underscored the need to better understand larval ecology and recruitment and the consequences of variable recruitment to benthic species assemblages. Named "supply-side ecology" (Lewin, 1986), this area of research has received increased attention recently, leading to a greater awareness of the importance of factors affecting the supply of recruits to adult populations (e.g., Underwood & Fairweather, 1989; Grosberg & Levitan, 1992).

Presently, evidence from a variety of sites has confirmed that the timing and magnitude of recruitment in marine systems is often highly variable and limiting. Variations in recruitment can substantially alter the nature and outcomes of post-recruitment processes and, ultimately, community structure. This recognition has forced a reconsideration of the generality of previously accepted community structure paradigms based only on post-recruitment interactions (e.g., Menge & Sutherland, 1987; Menge & Farrell, 1989; Roughgarden, 1989). The classical paradigm based on competition and predation was not invalidated *per se*, but rather its applicability was no longer considered universal to all regions (Roughgarden, 1989).

Most of the research on rocky intertidal communities has been conducted in temperate regions. Thus, ideas regarding the processes governing population dynamics and community structure have developed from experimentation under relatively favorable environmental conditions near the center of species' geographic distributions. Biological processes such as recruitment and species interactions are likely stronger and more consistent than near species' geographical limits where sub-optimal environmental conditions prevail.

On the northwest coast of North America, many rocky intertidal species have a broad geographical distribution, extending from northern California to high-latitude locations in southcentral and southwest Alaska. As a result,

rocky intertidal communities are compositionally similar along an environmental gradient spanning thousands of kilometers and 20° latitude. In Alaska, however, these communities exist in a climatic transition zone with longer winters having short photoperiods and periodic exposure to arctic air masses. Thus, the physical environment in southcentral Alaska is widely variable and less favorable to intertidal species, compared to lower, temperate latitudes. Consequently, a few species central to the formulation to of the competition and predation paradigms, especially the predatory sea star *Pisaster ochraceus* and the dominant space competitor *Mytilus californianus*, are absent or occur in such low densities that they do not play a significant role in structuring the community.

Without these key species, it would be important to know whether the community continued to be structured by post-recruitment events according to classical paradigms or if recruitment dynamics would dominate. Thus, the southcentral Alaska intertidal community, near the northern limit of distribution for many temperate intertidal species, presented an opportunity to experimentally evaluate the robustness of the classical predation-competition paradigm versus the importance of recruitment processes in generating and maintaining community structure.

CHAPTER 2

PHYSICAL AND BIOLOGICAL CHARACTERISTICS OF THE KACHEMAK BAY REGION: AN OVERVIEW

INTRODUCTION

Over 50% of the coastline and about 70% of the continental shelf area of the entire United States is located in Alaska. Habitats in the Alaskan coastal zone are diverse, productive, and dynamic and support a wide variety of commercial, subsistence, and recreational uses. Despite these important characteristics, relatively little is known about the ecological processes which are responsible for maintaining the structure of Alaskan coastal ecosystems. The general structure of marine habitats in Alaska has been described in a few large-scale studies (see Trasky *et al.*, 1977; Jarvela, 1982; Hood & Zimmerman, 1987), usually conducted in response to the possibility of oil development or a potentially threatened commercial fishery. However, fine-scale patterns of distribution and abundance of biological resources have not been well documented, nor have the underlying mechanisms responsible for generating such patterns been resolved. In particular, there is a notable paucity of knowledge about the ecological processes responsible for driving the dynamics of littoral communities in southcentral Alaska. Ecological processes in Alaska are likely to differ from those at well-studied coastal habitats elsewhere because seasonality is much more pronounced at higher latitudes.

The Lower Cook Inlet/Kachemak Bay region (Fig. 2.1) is an extremely productive marine ecosystem. It is a system having readily observable and

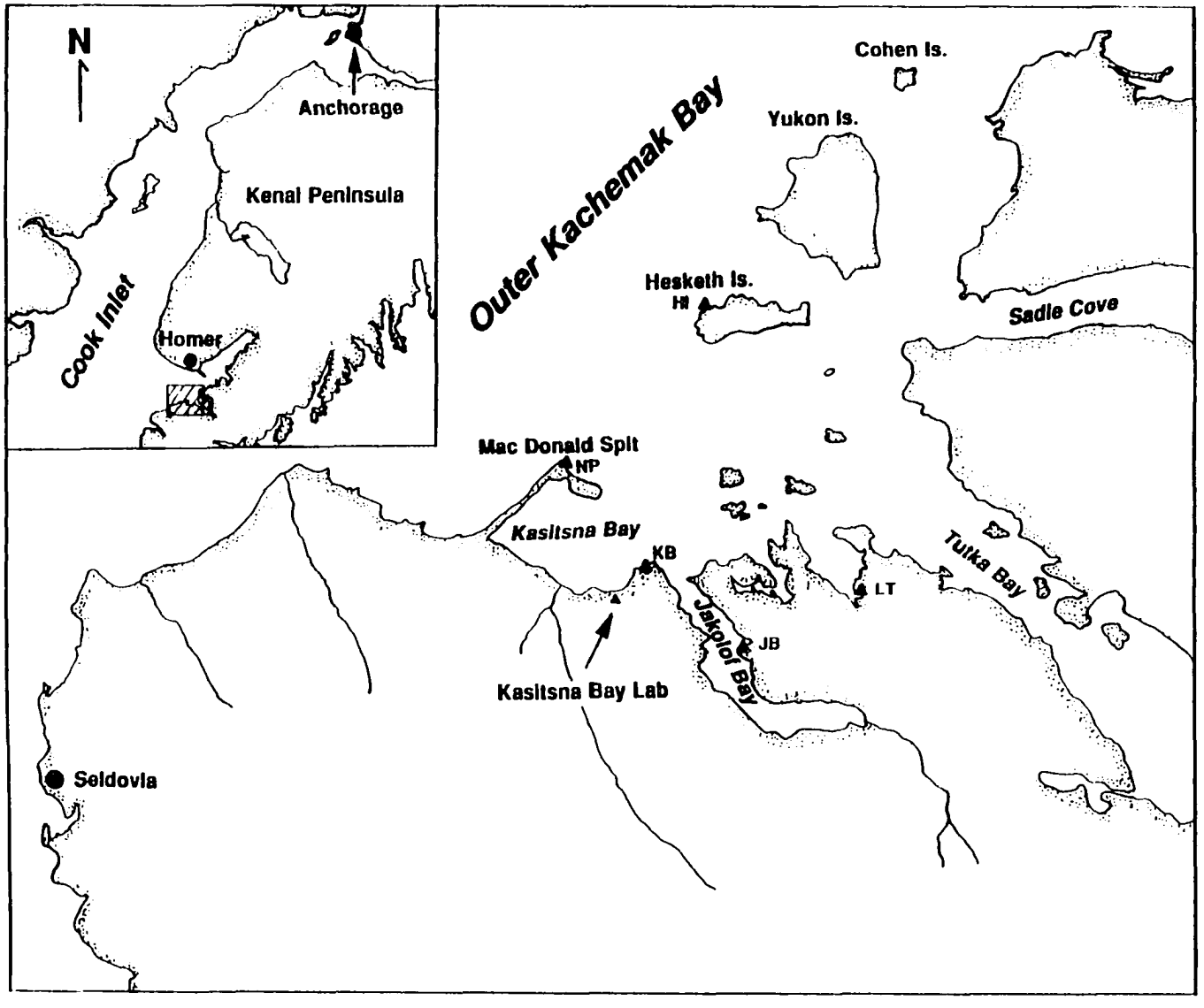

Figure 2.1: Map showing study sites on the south shore of Kachemak Bay, Alaska.

measurable changes in response to biological and physical phenomena, as seasonal transitions are abrupt and unmistakable and events occur quickly and with great intensity.

Seasonal extremes, high species diversity, and intense biological activity and cycles in Kachemak Bay provide an ideal setting for conducting ecological research. The littoral zones in this region possess many features that make them a highly significant part of the world's coastal habitat, yet our understanding of these zones is minimal. Wise use of marine resources demands a thorough understanding of the natural processes and phenomena which shape marine communities. Because the Alaskan coast constitutes over 85% of the west coast coastline, general theories of intertidal community structure will remain incomplete without an understanding of ecological processes responsible for regulating biological communities in Alaska. This study contributes to such an understanding by providing quantitative information on community structuring processes in southcentral Alaska.

PHYSICAL CHARACTERISTICS

Cook Inlet is a large tidal estuary located on the northwest edge of the Gulf of Alaska. Kachemak Bay (59° 35'N, 151° 30'W) is an elongated embayment contiguous to the southeastern entrance to Cook Inlet (Fig. 2.1). Kachemak Bay, 62 km in length and 38 km wide at its mouth, is oriented from

southwest to northeast. The bay is divided into inner and outer regions by the Homer Spit, a natural recurved sand spit which extends 7 km into the bay from the northern shoreline. The north shore is bounded by rolling hills and bluffs of the Kenai lowlands, while the south shore is bordered by mountains of the Kenai Range.

The unique geological characteristics on each side of Kachemak Bay result in different shoreline characteristics. The north shore consists of shallow mud flats interspersed with boulders and cobbles. Sand and clay cliffs rise rapidly from the shore, in some cases rising several hundred feet immediately adjacent to the shoreline. The southern side of the bay has greater water depths and the shoreline consists of mountainous, glacially eroded hardrock indented with many sheltered passages and both deep and shallow fjord-like bays. Many rocky islands occur near the south shore of the bay. The head of the bay is characterized by extensive tidal flats, braided drainages and marshlands. Large sediment loads are deposited into this portion of the bay by several major glacial streams.

Tectonic activity in and around Kachemak Bay is intense (Hayes *et al.*, 1977; Hood, 1987) because the Pacific plate subducts under the leading edge of the North American continental plate in this region. The result of this geologic phenomenon is a large number of active volcanoes and frequent earthquakes. Three separate volcanoes in the immediate vicinity of Cook

Inlet have erupted, some repeatedly, since 1986 (Mount Augustine [1986], Mount Redoubt [1989-1990], and Mount Spur [1992]). The Good Friday Earthquake of 1964 recorded a modern-record Richter Scale magnitude of 8.2. It's epicenter was located near the town of Valdez in Prince William Sound and it affected coastal areas throughout southcentral Alaska. The geologic result of this earthquake, which most affected coastal habitats, was sudden land-level changes of shorelines. Some shorelines in Prince William Sound were uplifted as much as 10 m, displacing the entire intertidal region to a position above the range of the tides (O'Clair & Zimmerman, 1987). However, in Kachemak Bay, subsidence of shorelines was more common, and Homer Spit subsided approximately 2 m. Effects of land-level changes on littoral communities were studied by Haven (1971), Johansen (1971), and Nybakken (1969, 1971).

Average water depth of Kachemak Bay is 46 m. A trench on the southcentral side of the bay reaches a depth of 176 m, but otherwise, the bottom is relatively flat or gently sloping. The benthic substrate of the bay at depths exceeding 20 m can be logically divided into four major geological facies (Driskell, Dames & Moore, 1977): shell debris (northern and southern shorelines of the outer bay), sand (central outer bay), muddy sand (central outer bay), and silt (central bay and inner bay). Of these facies, the richest infaunal and epifaunal assemblages were found associated with the shell

debris in the northern, outer bay.

The tidal regime is mixed semi-diurnal and the region has a notable tide range. In Kachemak Bay, the mean diurnal range is 4.7 m with an extreme range of 9-10 m. Water levels of 1.5 to 1.75 m below Mean Lower Low Water occur several times per year. In upper Cook Inlet, the tidal range during extreme spring tides can reach 12.5 m, which is the second greatest tide range in North America, exceeded only by the bay of Fundy in Nova Scotia. The result of the extreme tidal range is an oscillatory flow of water in Kachemak Bay corresponding to ebb and flood tides.

Superimposed on the tidal currents are net circulation patterns. Oceanic water derived from the Alaska Coastal Current enters Cook Inlet through Kennedy Entrance and is deflected by the coriolis forces into the south side of Kachemak Bay. The incoming water has low suspended sediments and high nutrients. Water may transit the bay, eventually exiting along the north shore back into Cook Inlet, or may be entrained by either of two semi-permanent gyres located in the central region of the outer bay (Fig. 2.2). As water transits the inner bay, salinity becomes reduced and sediment load is increased by runoff from numerous glacial streams emanating from the vast Harding Ice Field.

The regional climate is transitional between the temperate maritime climate characteristic of the northwest coast of North America and the

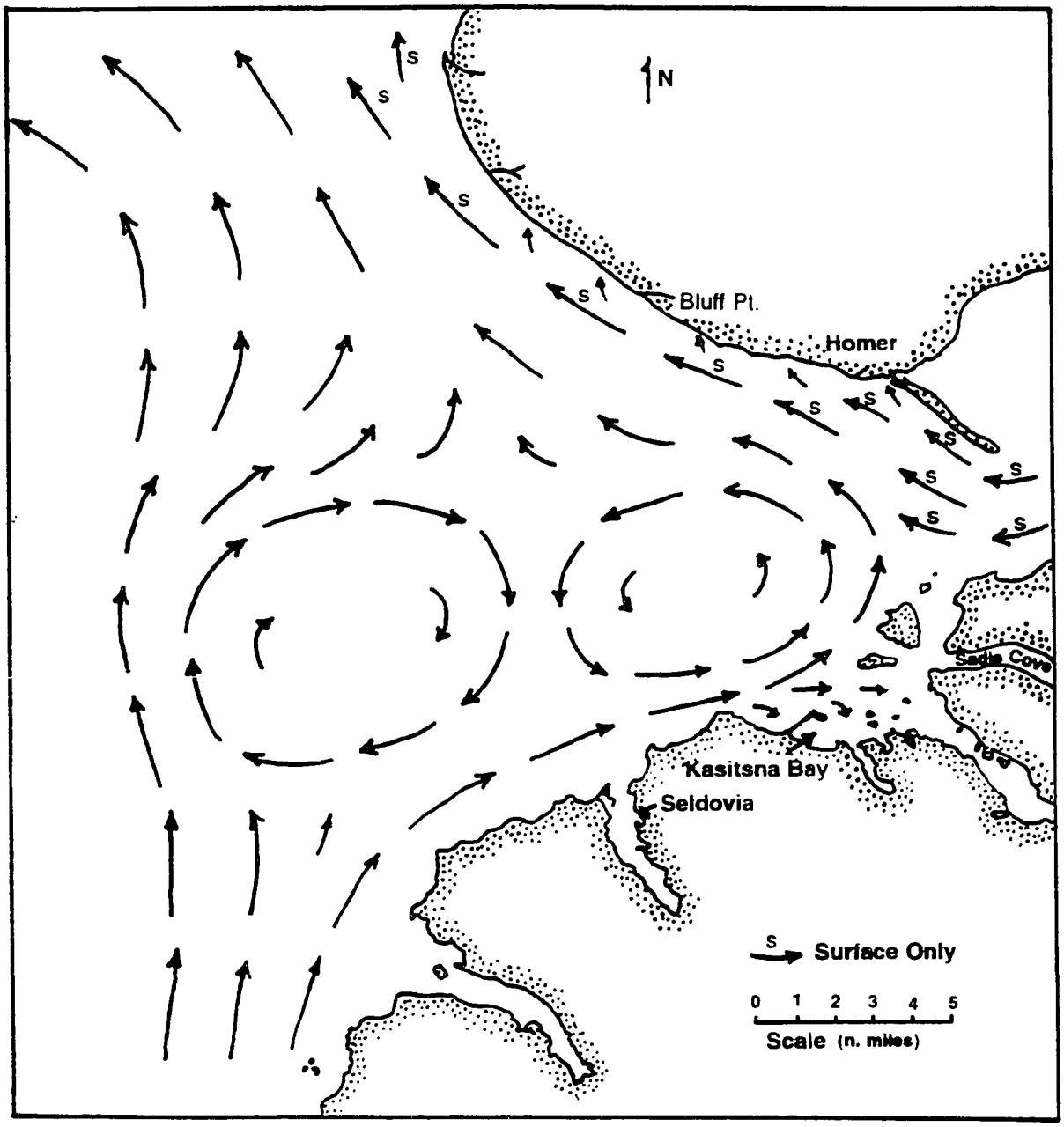

Figure 2.2: Map indicating the location of two permanent gyres in outer Kachemak Bay, Alaska (after Trasky *et al.*, 1977).

extreme sub-Arctic influences from interior Alaska. Summers are cool (6 to 15°C) and winters are relatively mild (-8 to +6°C). Air temperature extremes range from +27 to -31°C. Annual precipitation averages 71 cm of water including 257 cm of snow. Surface water temperatures on the south side of Kachemak Bay range from 14°C in July to 1.5°C in February (Fig. 2.3), with an annual mean temperature of 6.7°C. Winter storms are frequent, and winds may gust to 50-75 knots during any given year. Because of the moderating effect of the Gulf of Alaska, shore-fast ice is rare in Kachemak Bay. Occasionally, during severe winters, ice occurs along the northern shore of the inner bay as a result of freshwater input at the head of the bay.

There are two small communities located on Kachemak Bay: Homer (pop. 5000) is located on the north shore and Seldovia (pop. 350) on the south shore. Commercial and sport fishing, tourism, and recreation provide the economic foundation of these communities. There also exist numerous smaller settlements and villages along the bay's shorelines. The total population living around Kachemak Bay probably does not exceed 6000. Therefore, large-scale alterations of the marine ecosystem resulting from significant anthropogenic inputs to the bay seem unlikely.

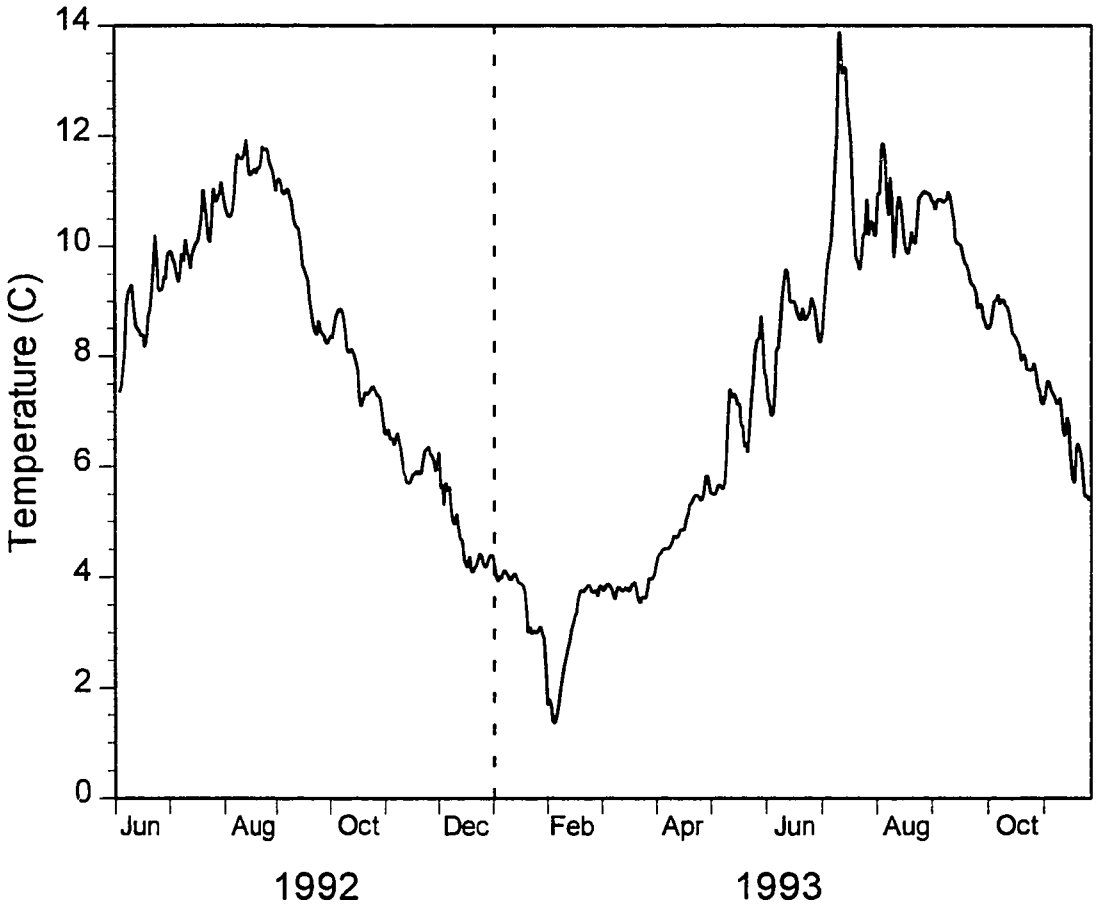

Figure 2.3: Sea surface temperature at Kasitsna Bay during 1992-1993. Temperatures are daily means of hourly recordings from an automated station 2 m below the sea surface. Overall water depth was approximately 10 m. The dashed vertical line delineates 1992 from 1993.

Biological Characteristics

Kachemak Bay is an extremely productive region with a remarkable variety of habitats and an extremely rich flora and fauna. The general abundance of organisms in the bay is unusually high, and the disproportionate number of commercial and recreational fisheries supported by the bay is striking. Marine species that are harvested commercially and/or recreationally in Kachemak Bay include: king crab, tanner crab, dungeness crab, five species of pandalid shrimp, all five species of Pacific salmon, halibut, herring, mussels and several species of clams. Additionally, a fledgling mariculture industry is beginning to produce oysters in commercial quantities. Kachemak Bay comprises less than 5% of the marine waters of the Cook Inlet Fisheries Management Area, yet it annually produces over 60% of the area's shellfish products. A total of 18 streams enter Kachemak Bay which serve as breeding locations for salmon stocks, and the bay's intertidal zones are critical importance as nursery grounds for pink salmon.

In addition to harvestable species, Kachemak Bay also supports a diverse assemblage of other conspicuous marine species. Sea otters are abundant (an estimated population of 400 in 1976; Schneider, 1976). Sea otters, because they lack a blubber layer under their skin, consume up to 30% of their body weight each day (Morrison *et al.*, 1974). Therefore, they occur in high abundance only in locations of plentiful food resources. In addition to

sea otters, moderately high densities of Dall porpoises, harbor porpoises and harbor seals are found in Kachemak Bay. Other marine mammals such as orca whales, beluga whales, minke whales and stellar sea lions are commonly found during certain months of the year.

Large populations of sea birds, shore birds, and waterfowl use the bay for feeding, nesting, and overwintering. In the spring and fall, the bay is an important migrational corridor for many species which breed in interior or Arctic Alaska but overwinter in more southerly locations. During migration seasons, over 1 million waterfowl have been counted during aerial surveys, which covered only a small portion of the bay (Ballard, 1976). Additionally, Kachemak Bay serves as the primary overwintering area for seabirds from Cook Inlet, accommodating 90% of the overwintering bird population. The value of outer Kachemak Bay to overwintering birds is probably directly related to food availability and the fact that it is the only ice-free bay in the lower inlet. During the summer, Kachemak Bay serves as an important nesting, feeding and rearing area for many species of marine birds and supports the highest seabird densities in Cook Inlet.

It is clear that the notable concentration of marine and associated species supported by Kachemak Bay is unique, both in diversity and sheer numbers. The exceptionally high biomass supported by the bay is dependent upon a unique combination of primary production cycles and energy transfer

processes which ultimately are driven by meso-scale current patterns and effects of the pronounced seasonality.

Water Column

The production patterns of Kachemak Bay are driven, in part, by the influence of the Alaska Coastal Current (ACC). The ACC flows northwest for 3000 km along the coastline from British Columbia to the Aleutian Islands and is the eastern and poleward boundary of the large-scale counter-clockwise rotating subarctic gyre (Reed & Schumacher, 1987). The ACC is a principle means by which warm maritime sea water is advected northward into Alaska, moderating the climate of coastal regions. The ACC is driven by large inputs of fresh water resulting from heavy precipitation and runoff in the Alaska Coastal Mountain Range, and current velocities exceed 100 cm sec^{-1} (Reed & Schumacher, 1987) in the region of the Kenai Peninsula. Low salinity, nutrient laden water from the ACC is advected into southern Kachemak Bay and carries with it plankton populations characteristic of the Gulf of Alaska as well as organic and inorganic particles. In Lower Cook Inlet, off the southwest tip of the Kenai Peninsula, upwelling occurs in summer months which adds additional nutrients to the water before it is carried directly into Kachemak Bay. Two semi-permanent gyres (Fig. 2.2) entrain some of this water and increase residence time of the plankton, particulates, and nutrients

advected from the ACC (Burbank, 1977). Residence time of water entering the gyre system is typically 1-2 weeks. This system concentrates and accelerates primary production and concentrates larvae. The gyre system, along with high freshwater runoff, are thought to stabilize the water column, allowing stratification and facilitating the development of algal blooms.

Hence, the circulation patterns in Lower Cook Inlet and Kachemak Bay, combined with the abundance of daylight in the summer (>19 hrs) result in high primary production rates in the water column and abundant deposition of organic matter to the benthos.

The beginning of the production cycle in Kachemak Bay is typical for higher latitude photic zones. A physically-mediated phytoplankton bloom occurs in the spring (usually early May) when light and nutrient conditions permit. However, instead of a typical decrease in primary production due to nutrient limitation as the summer progresses, in Kachemak Bay upwelling and entrainment by gyres maintain high nutrient levels throughout the summer. This results in daily primary production values as high as 7.7 gC m^{-2} and time-integrated annual production rates (based on measurements from May - August) exceeding 300 gC m^{-2} (Larrance *et al.*, 1977). These production values are 2 to 20 times greater than estimated production values of other locations in Cook Inlet (Larrance *et al.*, 1977) and place Kachemak Bay as one of the most productive marine ecosystems in the world

(Sambrotto & Lorenzen, 1987).

Of the annual primary production in Kachemak Bay, approximately 60 gC m^{-2} is delivered to the bottom (Chester & Larrance, 1981). Most of this flux (83%) is delivered in the form of zooplankton fecal pellets, with the remainder due to algal sinking. Plant biomass fluxes to the bottom in Kachemak Bay were also six times greater than for the remainder of Lower Cook Inlet. Therefore, although the phytoplankton and pelagic grazer populations are tightly coupled, large quantities of organic-rich particulate detrital material reach the bottom of Kachemak Bay.

A significant component of the zooplankton in the bay consists of larvae of various benthic groups including large numbers of commercially harvestable species. Zooplankton are retained in the bay by the aforementioned gyre system, keeping meroplankton concentrated in areas of abundant food resources. The reduced larval mortality and proximity to a suitable benthic habitat presumably result in greater recruitment to the benthos. Consequently, Kachemak Bay is an important nursery ground for planktonically dispersed benthic fauna, including commercially important species.

Intertidal Habitats

This section contains descriptions of major types of intertidal habitats in Kachemak Bay and indicates conspicuous species or assemblages present in each. Detailed discussion of the dynamics occurring between selected species will be the subject of subsequent chapters in this dissertation.

A typical means of categorizing intertidal habitats is by substrate type. Soft-bottom habitats are characterized by sandy or muddy substrates. Therefore, the opportunity exists for organisms to reside in the substrate (e.g. via burrowing). Hard-bottom habitats, in contrast, are characterized by impenetrable rock surfaces, creating a two-dimensional surface on which intertidal organisms live. Spatial heterogeneity is added by cracks, crevices, overhangs, and under-rock micro-habitats. Both soft- and hard-bottom habitats occur in Kachemak Bay.

Soft-bottom habitats in Kachemak Bay range from quiet, gently sloping muddy back-bays to exposed, steep cobble beaches. Moderately sloping beaches with sand or mud are the most common around Kachemak Bay and these habitats contain the highest faunal diversity of the soft bottom habitats. Although biotic diversity can be quite high in some of these soft-bottom habitats, distributions of individual species are usually restricted to specific micro-habitats by the physico-chemical properties associated with a specific locale (Kozloff, 1983). Therefore, habitat partitioning, both by depth in the

sediment and by sediment grain size (and resulting ability of the sediment to hold water, oxygen, food, and other biologically important compounds) is particularly common in soft-bottom areas. Bivalves are especially common in soft-bottom habitats, with several species partitioned by depth in the sediment: mussels (*Mytilus trossulus*) on the surface, cockles (*Clinocardium* spp.) just below the surface, and high densities of steamer clams (*Protothaca staminea*), *Macoma spp.*, soft-shell clams (*Mya arenaria*, *M. truncata*), and butter clams (*Saxidomus gigantea*) deeper in the sediment. Deep in sandy habitats, the large gaper clam (*Tresus capax*) is found. Infaunal bivalve densities of >100 m^{-2} are not uncommon. There is an extremely high diversity of other molluscs found in the bay (Foster, 1991), with 400 species having been identified from Kasitsna Bay alone, a small bay defined by McDonald Spit (Fig. 2.1) (Baxter, 1987). Additionally, a variety of polychaetes, nemerteans, sipunculids, echiurans, priapulids, holothurians, anemones, sea stars, and hermit crabs are commonly found associated with soft-bottom zones. The holothurian, *Cucumaria miniata,* can attain extremely high densities (>80 m^{-2}; R.C. Highsmith, unpublished data) in some locations. Dungeness crabs (*Cancer magister*), horse crabs (*Telmessus cheiragonus*), and sand dollars (*Echinarachnius parma*) are also locally abundant low in the intertidal. In very low energy, fine-sediment (clay or silt) locations, extensive eelgrass beds (*Zostera marina*) and salt marshes

(*Puccinellia hultenii*) may be found. Roots of these grasses stabilize the sediment and the detritus from their leaves is an important source of nutrients. Seagrasses are very productive and support a diverse community of epiphytes and infaunal species including the large burrow-dwelling echiurian, *Echiuris echiuris*.

Rocky intertidal habitats are often characterized by their exposure to wave action (Ricketts *et al.*, 1985; Stephenson & Stephenson, 1972). The hydrodynamic forces caused by waves considerably influence the biota found in a specific habitat (Kozloff, 1983) and the ecological processes responsible for structuring the local community (e.g. Paine, 1966, 1974; Menge, 1978a,b). Perhaps the most striking visual aspect of rocky shore communities in Kachemak Bay is the clearly defined vertical zonation patterns of species on the shoreline. This is a universal feature of rocky shores throughout the world (Stephenson & Stephenson, 1972). Distinct zonational bands are a result of a combination of the differing physiological tolerances of organisms to aerial exposure and of interactions with other organisms. It has been convincingly demonstrated that, in the majority of cases, the upper limit of an organism's distribution on a rocky shore is defined by its ability to withstand the physiological challenges associated with emersion (e.g. freezing, heating, respiration and desiccation), while the lower limit of most organisms is maintained by interactions with other organisms such as competition and

predation (e.g. Connell, 1961, 1970; Paine, 1966; review by Connell, 1972).

Although rocky intertidal species distributions in Kachemak Bay vary between sites in response to several physical and biological factors, many generalizations regarding species distributions can be made. Space is often the limiting resource in these communities. Thus, in contrast to soft-bottom communities, species are partitioned in rocky habitats by vertical position (tide height) on the shore rather than depth within the substrate. The following overview is an attempt to characterize general patterns and processes within Kachemak Bay, and therefore focuses upon distribution patterns of the most conspicuous and abundant species from highest to lowest in the rocky intertidal zone.

The supralittoral fringe is located at the extreme upper edge of the intertidal zone. Also called the splash zone, this region is rarely covered by the tide. Rather, it is usually only wetted by the splash of waves. The lichen, *Verrucaria*, is the dominant organism found in this zone and can be identified as a thin-layered black band on the rocks. The littorines, *Littorina scutulata* and *L. stikana*, are small herbivorous gastropods that may occur in the lower portion of this zone and extend lower into the intertidal. Occasionally, the barnacle *Chthamalus dalli* is also found this high. However, the distribution of *C. dalli* in Kachemak Bay is extremely patchy.

Just below the splash zone is the upper intertidal zone; the highest truly

intertidal zone. The rockweed, *Fucus gardneri*, is extremely abundant and often will cover the majority of space in this zone. The acorn barnacles, *Semibalanus balanoides* and *Balanus glandula*, are also found in this zone and can occupy considerable amounts of space. These barnacle species, similar in appearance, often occur together and are considered ecological equivalents in Alaska (O'Clair & Zimmerman, 1987), although this may not be the case at lower latitudes on the west coast (Carroll & Wethey, 1990). The littorines, mentioned above, are also common in this zone and occasionally form dense aggregations in which densities can be as high as 2.98×10^4 m^{-2} (Carroll, unpublished data). Other herbivores, such as the limpet *Tectura persona* also occur.

Lower yet is the mid-intertidal zone. This zone is often characterized by a dark, dense band of mussels, *Mytilus trossulus* (previously grouped with *M. edulis* [Koehn, 1991; McDonald *et al.*, 1991; Morgensen *et al.*, 1991]). *Fucus* also occurs in this zone, as do other macroalgae such as *Ulva sp.*, *Porphyra sp.*, *Halosaccion glandiforme*, and *Callophyllis sp.* The most common predators in this zone include the gastropod, *Nucella lima*, (see Chapter 5), the small six-rayed sea star *Leptasterias hexactis*, the crab *Cancer oregonensis*, and several species of nemerteans including *Paranemertes peregrina*, *Amphiporus imparispinosus*, *Emplectonema gracile* and *Tubulanus polymorphus.* Limpets are common herbivorous grazers found in

the lower part of this zone and include the species *Lottia pelta*, *L. digitalis*, and *Tectura scutum*. The vertical range of these limpets is large, and they also extend downward into the low intertidal zone.

In the low intertidal zone, much of the primary space is often occupied by the thatched barnacle, *Semibalanus cariosus*. In the summer months, there is a lush cover of kelps, primarily *Alaria fistulosa* and *Odonthalia spp.* In this zone, encrusting species such as sponges and bryozons are common. A principal herbivore at this intertidal level is the leather chiton, *Katharina tunicata*, though a variety of other chitons (*Mopalia spp.*, *Tonicella spp.*) and limpets also occur. *Katharina* is quite common and can reach densities >50 m^{-2} (Carroll, upublished data). Several species of sea stars are common in this zone, most notably *Evasterias troschelii*. In general, the sea star *Pisaster ochraceus* is rare or absent in Kachemak Bay and in the rest of southcentral Alaska. The predatory whelk, *Nucella lamellosa*, also occurs at this tide level and can be locally abundant though distributed patchily. Sea anemones become common in this level of the intertidal. Most common and conspicuous species include *Metridium senile*, *Anthopleura artemisia*, and *Urticina crassicornis*.

The lowest zone in the intertidal is the sublittoral fringe. Only exposed by the tide on rare occasions, species found here are principally true marine species with very limited tolerance to aerial exposure. The kelps, *Laminaria*

groenlandica and *Cymathere triplicata* are often very dense in the summer months and sometimes occur together with *Agarum cribosum*. Crustose coralline algae occupy much of the primary substratum. Other encrusting species are also common as are several species of ascidians. The colonial bryozoan *Membranipora membranacea*, is conspicuous in the late summer when it occurs in abundance as circular colonies on the flat blades of kelps. The sun star, *Pycnopodia helianthoides*, notable for its large size (>70 cm diameter) extends from the lower intertidal into the subtidal. Algae in this zone are grazed principally by the green sea urchin *Strongylocentrotus droebachiensis*. The limpet, *Acmea mitra*, is found at this tide level, often with crustose coralline algae encrusting its shell. Serpulid and spirorbid polychaetes are common and can often be found in crevices, tidepools, and on the underside of rocks. Occasionally, large (up to 30 cm in length) gumboot chitons, *Cryptochiton stelleri*, and large sea cucumbers, *Parastichopus californicus*, are observed.

Several species of crabs and hermit crabs (including *Telmessus cheiragonus*, *Cancer oregonensis*, *Oregonia gracilis, Hapalogaster mertensii*, *Pagurus spp.*, *Elassochirus spp.*) occur throughout the mid- to lower rocky intertidal zone of Kachemak Bay.

A comprehensive listing of local species is presented in Table 2.1. It includes both benthic macrofauna and macroalgae found in Kachemak Bay

intertidal zones. The list was originally published in Dames & Moore (1977) and has been modified and updated to include the observations of R.C. Highsmith and this author during their field work in Kachemak Bay.

Table 2.1a: Benthic macroinvertebrates of Kachemak Bay. List was originally published by Dames & Moore (1977) and has been updated based on observations by R.C. Highsmith and the author during field work in the region.

PORIFERA:

Bathydoris dawsoni (?)
Cliona celata
Cydonium mulleri
Esperiopsis laxa
Esperiopsis rigida
Halichondria panicea
Haliclona permollis
Iophon sp. (?)
Ophlitaspongia pennata
Suberites ficus

CNIDARIA:

Abietinaria sp.
Aglaophenia sp.
Anthopleura artemisia
Aurelia sp.
Bougainvillia sp.
Calycella syringa
Campanularia verticillata
Cariophyllia alaskensis
Chrysaora melanaster
Cyanea capillata
Diadumene sp.
Epiactis prolifera
Eutonina indicans
Halecium marsupiale
Lafaea fruticosa
Metridium senile
Obelia sp.
Sertularella tricuspidata
Tubularia sp.
Urticina crassicornis
Urticina lofotensis
Urticina sp.

PLATYHELMINTHES:

Notoplana sp.
Kaburakia sp.

NEMERTINA:

Amphiporus imparispinosus
Cerebratulus sp.
Emplectonema gracile
Paranemertes peregrina
Tubulanus polymorphus
Tubulanus sexlineata

PRIAPULIDA:

Priapulus caudatus

ANNELIDA:

Aberinicola pacifica
Amphitrite groenlandica
Arabellidae, unid.
Arctonoe vittata
Axiothella rubrocincta
Crucigera sp.
Eudistylia (?) polymorpha
Eudistylia vancouveri
Flabelligera affinis
Glycera sp.
Halocydna brevisetosa

Harmothoe extenuata
Maldanidae, unid.
Myxicola infludibulum
Nephtys sp.
Nereidae, unid.
Nereis vexillosa
Nereis zonata
Owenia (?) collaris
Pectinaria (Cistenides) granulata
Pholoe minuata
Pholoides aspera
Phyllodoce sp.
Polynoidae, unid.
Potamilla neglecta
Potamilla rienformis
Pseudopotamilla occelata
Seaella crassicornis
Sabella sp.
Sabellidae, unid.
Serpula cf. vermicularis
Spirorbis spp.
Sternaspis acuta
Syllidae, unid.
Terebellides stroemi
Thelepus cincinnatus
Thelepus crispus
Typosyllis sp.

SIPUNCULA:

Golfingia margaritacea
Phascolosoma agassizzi

ECHIURA:

Bonellia viridis
Eubonellia valida
Echiuris echiuris alaskanus

MOLLUSCA:

Acmaea mitra
Acanthodoris nanaimoensis
Aeolidia papillosa
Amphissa columbiana
Archidoris montereyensis
Archidoris ohdneri
Anisodoris nobilis
Armina californica
Astarte undata
Austrodoris sp. (?)
Buccinum baeri
Buccinum glaciale
Cadlina luteomarginata
Calliostoma ligatum
Chlamys sp.
Clinocardium californiense
Clinocardium nuttallii
Crepidula sp.
Cryptobranchia spp.
Cryptochiton stelleri
Cylichna sp.
Dendrontus dalli
Dendrontus frondosus
Diodora aspera
Dirona albolineata
Discodoris sandiegensis
Doridella steinbergae
Entodesma saxicola
Eubranchus sp.
Flabellina verrucosa
Fusitriton oregonensis
Glycymeris subobsoleta
Hermissenda crassicornis
Hiatella arctica
Humilaria kennerleyi
Ischnochiton albus
Katharina tunicata
Lacuna sp.
Leptochiton rigatus
Littorina scutulata

Littorina sitkana
Lottia digitalis
Lottia pelta
Macoma balthica
Macoma inquinata
Macoma nasuta
Margarites pupillus
Melanochlamys diomedea
Melibe leonina
Modiolus modiolus
Mopalia ciliata
Mopalia lignosa
Mopalia muscosa
Musculus discors
Mya arenaria
Mya truncata
Mya sp.
Mysella planata
Mytilus trossulus
Natica lutica
Neptunea lirata
Nucella canaliculata
Nucella emarginata
Nucella lamellosa
Nucella lima
Octopus dofleini
Onchidella borealis
Placiphorella velata
Placiphorella spp.
Pododesmus macroschisma
Protothaca staminea
Puncturella multistriata (?)
Rossia pacifica
Rostanga pulchra
Saxidomus giganteus
Searlesia dira
Serripes groenlandica
Serripes laperousii
Siphonaria thersites
Spisula polynyma
Tectura fenestrata
Tectura persona
Tectura scutum
Tellina nuculoides
Tonicella lineata
Tonicella insignis
Tresus capax
Trichotropis cancellata
Trophonopsis canellata
Trophonopsis pacificus
Triopha carpenteri
Velutina sp.
Volutharpa ampullacea

ARTHROPODA:

Amphipoda (Gammaridea), unid.
Amphipoda (Caprellidaea), unid.
Balanus crenatus
Balanus glandula
Balanus nubilis
Cancer magister
Cancer oregonensis
Cancer productus
Caprella sp.
Chionoecetes bairdi
Cryptolithodes stichensis
Chthamalus dalli
Elassochirus gilli
Elassochirus tenuimanus
Gnorimosphaeroma oregonensis
Gracilis oregonia
Hapalogaster mertensii
Hyas lyratus
Idotea wosnesenskii
Leptochelia dubia
Mysidacea, unid.
Oregonia gracilis
Orthopagurus minimus
Pagurus confragosus
Pagurus ochotensis
Pandalus borealis
Paralithoides camtschatica

Peltogasterella gracilis
Pinnixa faba
Pugettia gracilis
Pugettia producta
Saduria entomon
Semibalanus balanoides
Semibalanus cariosus
Scyra acutifrons
Telmessus cheiragonus
Traskorchestia traskiana

BRACHIOPODA:

Diestothyris frontalis (?)
Hemithyris psittacea (?)
Terebratalia transversa
Terebratulina sp.

BRYOZOA:

Alcyonidium sp.
Carbasea carbasea
Dendrobeania murrayana
Flustrella gigantea
Heterpora sp.
Hippodiplosia sp.
Membranipora membranacea
Microporina borealis
Myriozoum subgracile
Rhynchozoon sp. (?)
Schizoporella sp.

ECHINODERMATA:

Chiridota sp.
Crossaster papposus
Cucumaria miniata
Cucumaria vegae
Cucumaria piperata
Dermasterias imbricata
Echinarachnius parma
Eupentacta quinquesemita
Evasterias troschelii
Henricia leviuscula
Henricia sanguinolenta
Henricia tumida
Leptasterias hexactis
Leptasterias polaris (var. aceruata)
Lethasterias nanimensis
Ophiopholis aculeata
Orthasterias koehleri
Parastichopus californicus
Pisaster brevispinus
Psolus chitonoides
Pteraster tesselatus
Pycnopodia helianthoides
Solaster dawsoni
Solaster stimpsoni
Strongylocentrotus droebachiensis
Strongylocentrotus franciscanus
Strongylocentrotus pallidus
Strongylocentrotus purpuratus
Tosiaster arcticus

UROCHORDATA:

Aplidium solidum
Boltenia villosa
Botryllus sp.
Chelysoma sp.
Cnemidocarpa finmarkiensis
Corella sp. (?)
Gersemia rubiformis
Halocynthia aurantium
Metandrocarpa taylori
Ritterella pulchra
Styela gibbsi
Styela montereyensis
Synoicum parusti

Table 2.1b: Benthic macroalgae of Kachemak Bay. List was originally published by Dames & Moore (1977) and has been updated based on the observations of R.C. Highsmith and the author during their field work in the region.

CHLOROPHYTA:

Codium ritteri
Enteromorpha (clathrata)
Enteromorpha intestinalis
Enteromorpha linza
Halicystis ovalis
Monostromata fuscum
Monostromata oxsperum
Prasiola meridionalis
Rhizoclonium riparium
Spongomorpha saxitalis
Ulva (expansa)
Ulva (lactuca)

PHAEOPHYTA:

Agarum criborosum
Alaria fistulosa
Alaria (praelonga)
Chorda filum
Chordaria gracilis
Costaria costata
Cymethere triplicata
Desmarestia ligulata
(var. ligualta)
Desmarestia viridis
Dictyosiphon foeniculaceus
Fucus distichus
Fucus gardneri
Fucus spiralis
Hedophyllum sessile
Laminaria groenlandica
Laminaria saccharina
Leathesia difformis
Melanospihon intestinale
Nereocystis luetkeana
Petalonia fascia
Pilayella littoralis
Ralfsia fungiformis
Scytosiphon lomentaria
Soranthera ulvoidea

RHODOPHYTA:

Acrochaetium sp.
Ahnfeltia plicata
Bossiella cretacea
Bossiella sp.
Callithamnion pikeanum
(var. pacificum)
Callithamnion or
Plenosporium sp.
Callophyllis edentata
Callophyllis flabellutata
Callophyllis haenophylla
Callophyllis sp. A
Constantinea simplex
Corallina frondescens
Corallina vancouveriensis
Cryptonemia borealis
Cryptonemia obovata
Cryptosiphonia woodii
Delesseria decipens
Dilesia californica
Endocladia muricta
Euthora fruticulosa
Gigartina papillata
Halosaccion glandiforme
Halymenia coccinea

Heterochordaria abietinia
Heterosiphonia laxa
Hildenbrandia protypus
Iridea (cornucopiae)
Iridea heterocarpa
Kallymenia oblongifructa
Lithothamnion sp.
Lithothrix aspergillum
Membranoptera weeksiae
Microcladia borealis
Neodilsea americana
Neodilsea integra
Odonthalia floccosa
Odonthalia kamtschatica
Odonthalia (washingtoniensis)
Opuntiella californica
Palmaria mollis
Petrocelis franciscana
Phycodrys sp.
Platythamnion sp.
Polysiphonia hendryi (var. luxurians)
Polysiphonia pacifica
Polysiphonia urceolata
Porphyra amplissima
Porphyra nereocystis
Porphyra sp. #1
Porphyra sp. #2
Porphyra sp. #4
Ptilota (filicina)
Rhodomela larix
Rhodymenia liniformis
Rhodymenia palmata
Rhodymenia pertusa
Scagelia occidentalis
Schizymenia borealis
Schizymenia epiphytica
Turnerella mertensiana

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CHAPTER 3

PATTERNS OF VARIATION IN SPECIES COVER: SEASONALITY, SUCCESSION, AND RECOVERY FROM DISTURBANCE

INTRODUCTION

A principal focus in ecological studies of natural systems is to identify patterns exhibited by populations in a community and to determine the processes responsible for creating them (Wiens, 1984; Wilbur & Travis, 1984). However, experimental studies often proceed in investigating structural processes without fully defining the pattern of interest. Observations are often restricted spatially and temporally by a variety of external influences including time limitations and funding constraints, so long-term background work on a given system is often given low priority or ignored. As a result perceived patterns often result from "snapshot" views at the time experimental work is conducted and therefore do not incorporate historical effects or longer term cycles that may have played an important role in generating such patterns. Especially worrisome is the assumption implicit in relatively short-term observations that the communities being observed are in equilibrium in the sense of their stability or the steadiness of community components (Wiens, 1984). In some cases, this assumption is realistic, but more often, especially where physical factors are not constant and predictable, this assumption is invalid. The result is that "...patterns that are detected by application of an equilibrium-based methodology to a non-equilibrial community have a strong likelihood of being more myth than reality" (Wiens, 1984 p. 453).

Another shortfall of short-term experimental studies is the lack of baseline data they provide regarding the structure and functioning of communities of interest in an undisturbed and unmanipulated state. Anthropogenic impacts are occurring on a global scale (e.g. Bolin *et al.*, 1986; Houghton *et al.*,

1990). In coastal marine communities, human encroachment resulting from population growth or movements, industry, and recreation has led to an accelerated frequency of habitat alteration. There is a critical need for long-term studies which characterize community patterns and structuring processes in an undisturbed state. Such baseline data are necessary for accurate assessment of the magnitude and consequences of future human impacts as well as natural disturbances. The lack of information on the characteristic patterns and processes occurring in the Alaskan intertidal became especially clear after the *EXXON VALDEZ* oil spill in Prince William Sound in March 1989. The intertidal zone was profoundly affected by grounded oil and subsequent clean-up activities, yet there were few data characterizing the community and its structuring processes before the spill, so assessment of the damage to the system was particularly difficult, if not impossible to determine.

Long-term, non-manipulative studies conducted over extended scales of time and space fill an important need by providing data on long-term patterns and cycles in species distribution, abundance, and interactions, and may also reveal the importance of rare but intense perturbations. This type of information, combined with experimental studies, provides a more complete assessment of the system being studied than either approach could provide alone.

This paper reports the results of a multi-year, non-manipulative field study designed to establish patterns of variation in species cover in the rocky intertidal community of Kachemak Bay, southcentral Alaska (59° 35'N, 151° 30'W). The cover of space-occupying species was tracked by monthly

censuses of permanent quadrats for almost 4 years. Although intertidal communities in Kachemak Bay are similar to those at lower latitudes on the west coast, physical extremes are clearly greater at high latitudes. Seasonal variation in temperature and photoperiod are more pronounced at this mid-Alaskan latitude than at more temperate locations, yet the effects of such seasonality on patterns of distribution, abundance, and interactions between resident species are unknown.

Additionally, the structure of the Kachemak Bay intertidal community was impacted by a severe cold snap in January 1989, a few months before the initiation of this study. Air temperatures were below normal for 25 consecutive days in January and early February 1989, with 19 consecutive days >5°C below normal. Temperature anomalies as great as -21°C occurred when ambient temperatures dropped to -31°C (Fig. 3.1), the lowest air temperature recorded in 60 years of data (NOAA, 1994). Lowest tides during the period exceeded 1.0 m below datum, and low tides of +1.3 m occurred during the coldest period (Fig. 3.1), exposing two-thirds of the intertidal zone to severe temperature extremes. The occurrence of this acute, stochastic disturbance provided an opportunity to examine community recovery and to observe successional changes during recovery.

The goals of this study were three-fold: (1) to document long-term patterns of intertidal species variation in a community with a physical regime having strong seasonal signals, (2) to determine the rate of recovery of the community from a severe disturbance, and (3) to examine any successional changes during recovery.

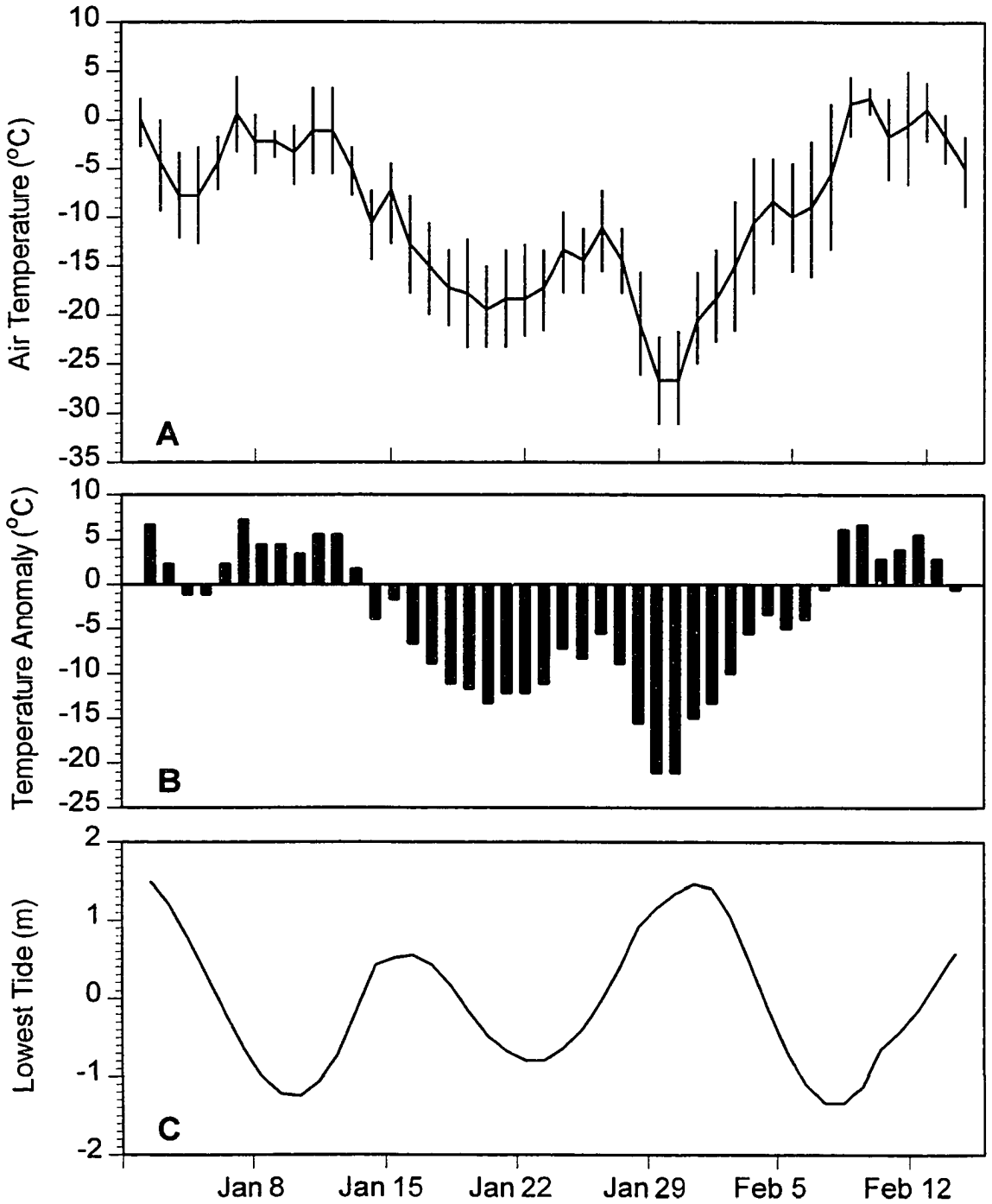

Figure 3.1: Temperature and tide data from Homer, Alaska during January and February 1989. Daily average temperatures and temperature range (indicated by bars)(A), the deviation from historical average temperatures (a negative anomaly indicates colder than normal temperatures) (B), and the lowest daily tide level during that time period (C).

This study was designed to serve as a multi-year baseline for the development and experimental testing of hypotheses regarding mechanisms of population regulation of specific members of the community and its overall structure. Time-series monitoring was conducted to establish patterns of spatial abundance of major intertidal species, to identify variations in cover of species, and to determine time scales of variations, e.g. seasonal, intra-annual, and inter-annual.

METHODS

Study Sites

Four sites were chosen based on their relative exposure to wave action (Fig. 2.1). Hesketh Island (HI) is the most exposed of the four sites. The Island is exposed to waves generated across the entire width (150 km) of lower Cook Inlet and in some cases to waves originating in the Gulf of Alaska. However, the site is not exposed to extreme high-energy waves or the constant wave action characteristic of outer coast shorelines. Kasitsna Bay Point (KB) is exposed to relatively moderate wave action, especially during winter, but is protected from the prevailing wind direction and long-fetch waves of Cook Inlet by McDonald Spit. Jakolof Bay (JB) and Little Tutka Bay (LT) sites are located inside sheltered embayments and thus are free from all significant wave action. These embayments are, however, subject to relatively high tidal currents, especially during spring tides which can range up to 9-10 m. (Dames & Moore, 1977).

Sampling Procedure

A vertical transect was established at each site in July 1989. Two additional transects were established 5-10 m away from the original in July 1990 at all sites except Little Tutka. At Little Tutka, there was not enough suitable rock surface to establish additional transects. Because of the lack of replication at Little Tutka, the results from this site are discussed separately.

Along each transect line, four permanent 0.25 m^2 quadrats were established at 1.5 meter vertical intervals from +4.5 m down to 0.0 m (MLLW). This placement of quadrats corresponded roughly to the zonation patterns of several major intertidal associations in this region (e.g. barnacle zone, mussel zone, etc.). In Kachemak Bay, the rocky intertidal is characterized by outcrops with abundant boulders and cobbles. These formations result in a paucity of large, flat expanses of rock suitable for the establishment of permanent quadrats. Therefore, it was often necessary to move off the transect line a short distance to find enough suitable rock surface to locate a quadrat. Corners of quadrats were permanently marked with stainless steel screws and large washers which were anchored in the rock with plastic wall anchors imbedded into holes drilled with a gas-powered pneumatic drill (Ryobi roto-hammer).

Hereafter, the terms tidal height or tide level indicate the fixed vertical location in the intertidal zone in which a quadrat is located. Level 1 refers to the uppermost level (+4.5 m) in the intertidal at which permanent quadrats were located, with levels 2, 3, and 4 referring to quadrats at +3.0 m, +1.5 m, and 0.0 m, respectively.

Quadrats were censused generally every 2-3 months to determine cover. Censuses were conducted more frequently in summer than in winter because of logistical and weather-related considerations in winter. No censuses were conducted during the winter of 1989-90 and 1992-93, therefore seasonal variations during those periods may not be reflected in the time-series cover plots (Figs. 2.3-2.8). The quadrats were censused for species cover using the point frame method for cover estimation. A 0.25 m^2 frame was placed over each quadrat and aligned with the corner screws and photographed with a Nikonos V camera with attached strobe light using Kodachrome 64 or Ektachrome 100 film. The resulting slides of each quadrat were projected back to 100% actual size and were overlain with an 81 point grid. Abundance of each cover group was estimated by dividing the number of points directly over that group by the total number points in the grid (Littler & Littler, 1985). By this convention, each point in the grid represents 1.23% of the quadrat area. To test the variability introduced by this method, several slides of quadrats were chosen at random and were repeatedly censused (n=30 per slide) with slightly different orientations of the overlay grid. An analysis of the variation in these data revealed that error associated with using this method was ±3.5%.

Quadrats were censused to determine variations in areal cover of major space-occupying species or functional groups of species. Six categories were utilized: BARNACLES (high shore barnacles including *Balanus glandula* and *Semibalanus balanoides*. *Chthamalus dalli* was not observed in any quadrat), *FUCUS* (the rockweed *Fucus gardneri*; see Scagel *et al.*, 1989 for current nomenclature), MUSSELS (*Mytilus trossulus*; see Koehn, 1991;

McDonald *et al.*, 1991; Morgensen *et al.*, 1991 for current nomenclature), CARIOSUS (*Semlbalanus cariosus.* This barnacle was separated from the high shore barnacle group because its distinct morphology and distribution patterns are different from the other barnacles), OTHER MACROALGAE (primarily foliose red and leafy green algae such as *Ulva sp.*, *Callophyllis spp.*, and *Odonthalia spp.* in the mid-tide levels and foliose reds and large brown kelps in the lowest zones, e.g. *Odonthalia spp., Alaria fistulosa, and Laminaria groenlandica*). TOTAL COVER is the summed cover of the five groups in a given quadrat. The data collected were analyzed to determine vertical distributions, seasonal variations in cover, and successional trends.

Statistical Analysis

Cover data were first arcsine square-root transformed to normalize the distribution of percentage data. Since the same quadrats were sampled repeatedly through time, the censuses could not be considered independent samples. Therefore, data were analyzed using repeated measures analysis of variance. All analyses were conducted using SAS for PC, version 6.04 (SAS, 1988). All figures and tables present untransformed data for graphical clarity and consistency.

RESULTS

Vertical Distribution and Cover

Despite some variation in vertical distribution of species depending on the site and season, species groups examined in this study characteristically occurred at well-defined vertical locations in the intertidal (Fig. 3.2).

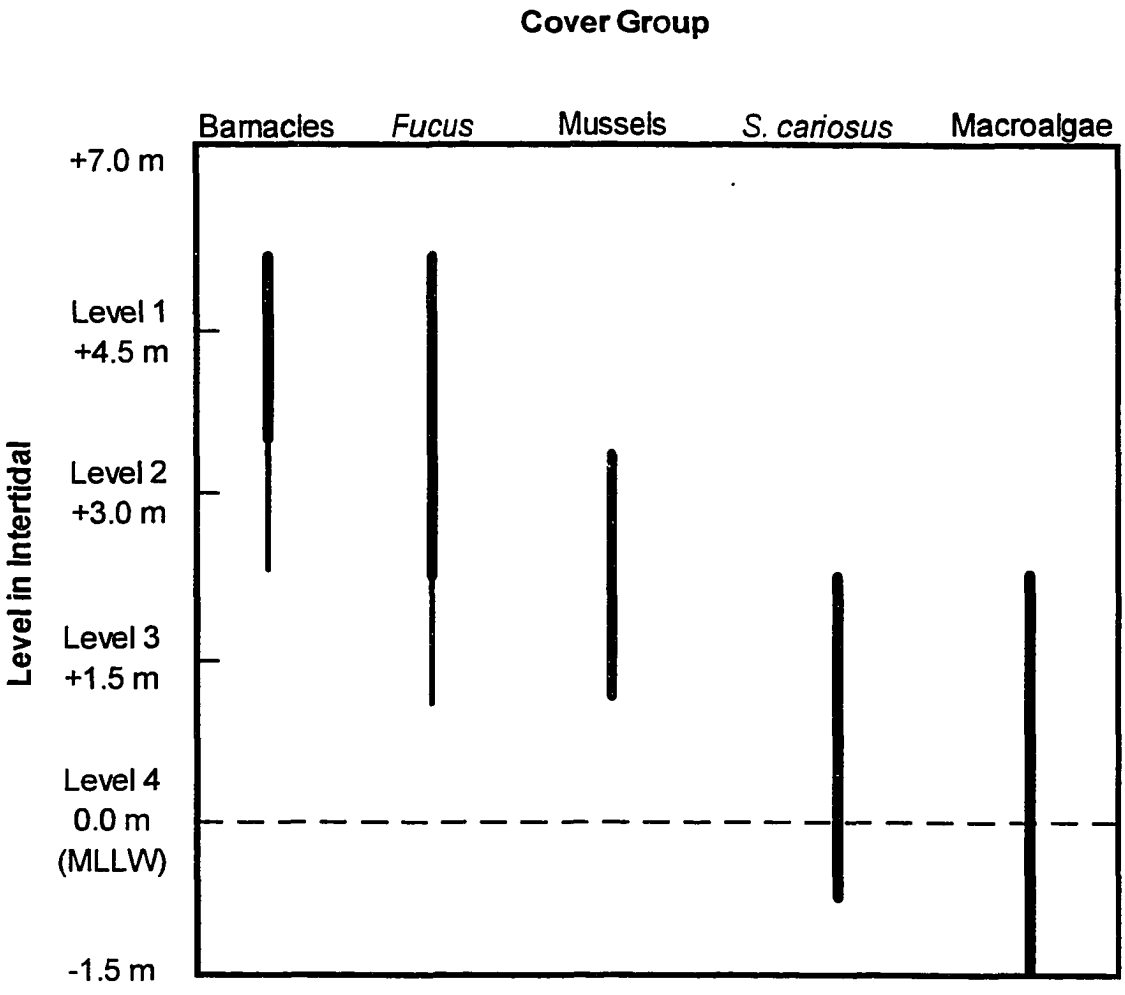

Figure 3.2: Vertical distribution of cover groups censused in the permanent quadrats. Heavier lines designate the tide levels of a cover group's greatest abundance and lighter lines indicate lesser abundance. See text for details of composition of cover groups.

Fucus gardneri exhibited a greater vertical range of coverage than the other cover groups which tended to be most common over one or two intertidal levels. *Fucus* was the dominant cover type in the two uppermost intertidal levels and was commonly found in the lower middle level as well. In contrast, mussels occupied a narrower vertical range than other groups. The limited distribution of mussels in this study contrasts Suchanek (1986) who observed that *M. trossulus* (Suchanek used the name *M. edulis*) occupied up to 5.5 vertical meters of intertidal substrate in Glacier Bay, Alaska. The observed distribution patterns of mussels in Kachemak Bay may reflect mortality associated with the severe freeze in January 1989 (see below; Chapter 5).

BARNACLES: The barnacle group is composed of *Semibalanus balanoides* and *Balanus glandula*. These species were considered together as one functional group because they are difficult to differentiate when young, they co-occur at all of the study sites, and are considered ecological equivalents in the Alaska (O'Clair & Zimmerman, 1987). Initial census of the permanent quadrats in 1989 revealed extensive barnacle cover in the upper two tidal levels at all sites (Fig. 3.3). All barnacles were uniformly small, indicating that they were recent recruits. The heavy barnacle set and cover (>95% in some areas) may have resulted from the general availability of free space resulting from the extensive mortality of intertidal organisms during the catastrophic freeze in January of that year (see discussion). The heavy barnacle set, combined with the absence of other organisms, resulted in a virtual monoculture of barnacles in the upper two intertidal levels. Barnacle cover subsequently exhibited a steady decrease at all sites for approximately two

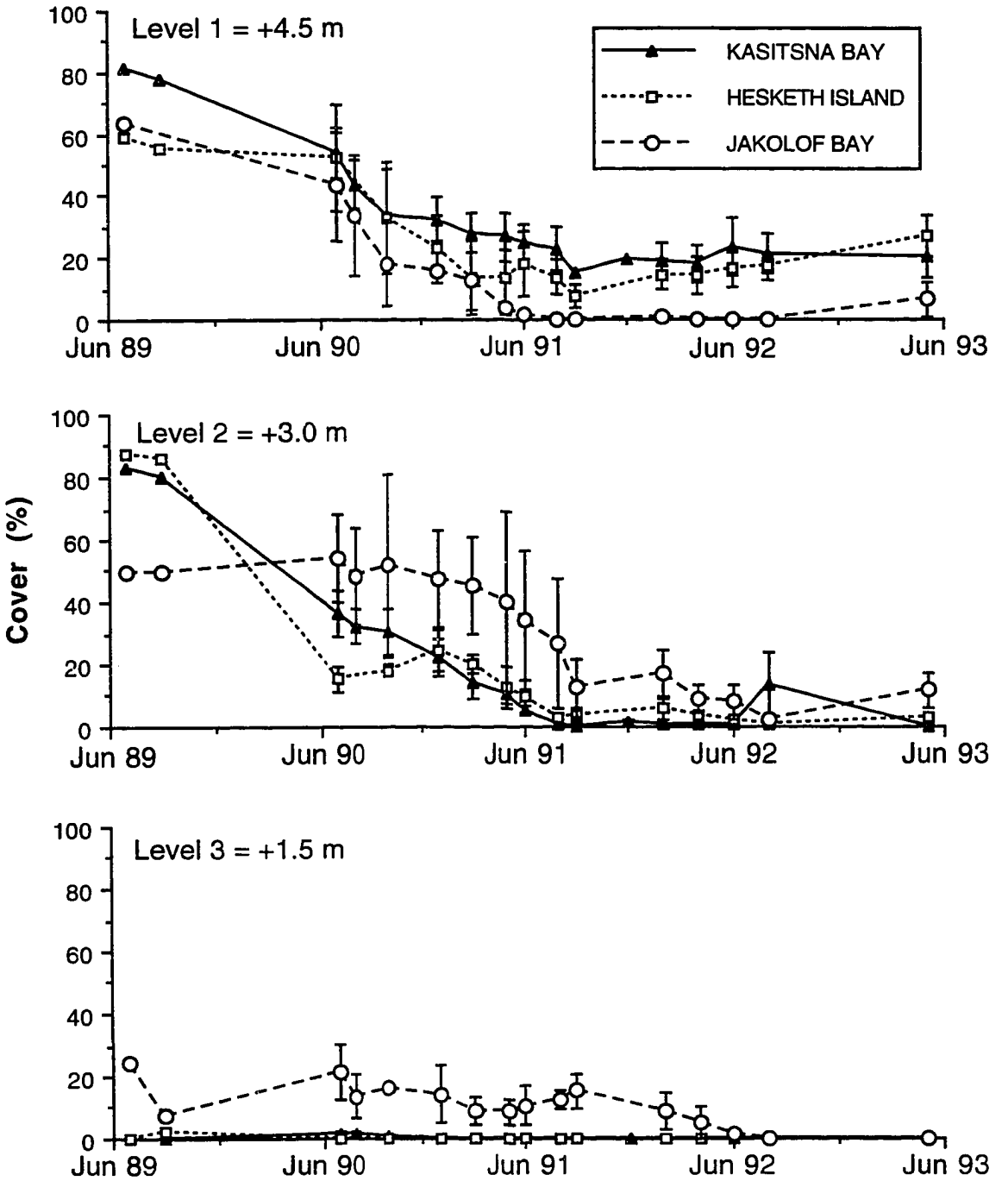

Figure 3.3: Mean cover (%±SE) of the barnacles *Balanus glandula* and *Semibalanus balanoides* at 3 sites in Kachemak Bay. Relative exposure of sites to wave action is Hesketh Island > Kasitsna Bay > Jakolof Bay.

years as space was recolonized by other species (see below). During the summer of 1991, barnacle cover stabilized at 20% or less. High levels of recruitment in 1992 and 1993 (see Chapter 4) were insufficient to overcome mortality and significantly increase barnacle cover in the final two years.

***Fucus*:** At all sites, *Fucus gardneri* initially occupied <20% of space and in many quadrats was completely absent (Fig. 3.4). *Fucus* cover increased rapidly through September 1990, reaching 40-50% at the upper level and 30% in the upper-mid level. *Fucus* cover eventually stabilized at Hesketh Island and Kasitsna Bay, with slight increases in summer offset by decreases of similar magnitude during the winter months. At Jakolof Bay, however, *Fucus* cover steadily increased in the two upper levels, reaching 100% cover at level 1 and >80% cover at level 2. At the level 3, *Fucus* cover was minimal at all sites through July 1991, then increased about 35% at the most protected site. This coincided with spring increases in *Fucus* cover at other tidal heights. Cover dominance by *Fucus* was maintained until the winter of 1992-1993 when *Fucus* cover appreciably declined at all intertidal levels, a trend particularly noticeable, however, at level 3.

MUSSELS: *Mytilus trossulus* initially occupied virtually no space within their normal intertidal range (Level 2 in Fig. 3.5). In April 1989, before permanent quadrats were established, a reconnaissance revealed dense beds of gaping mussels and extensive windrows of many thousands of mussel shells on beaches. These observations combined with the lack of mussel cover in the quadrats in 1989 suggest severe mortality associated with the January 1989 freeze.

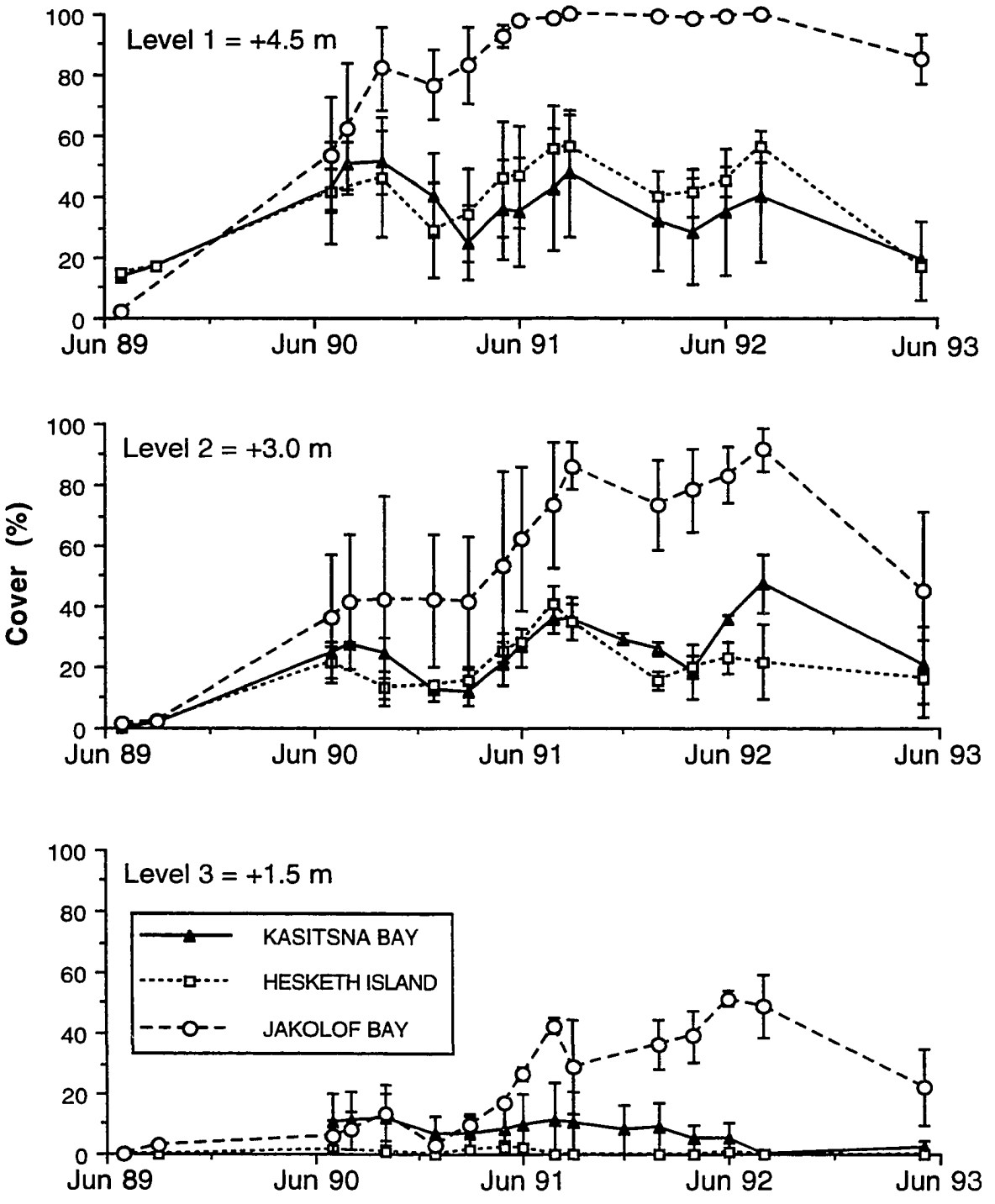

Figure 3.4: Mean cover (%±SE) of *Fucus gardneri* at 3 sites in Kachemak Bay. Relative exposure of sites to wave action is Hesketh Island > Kasitsna Bay > Jakolof Bay.

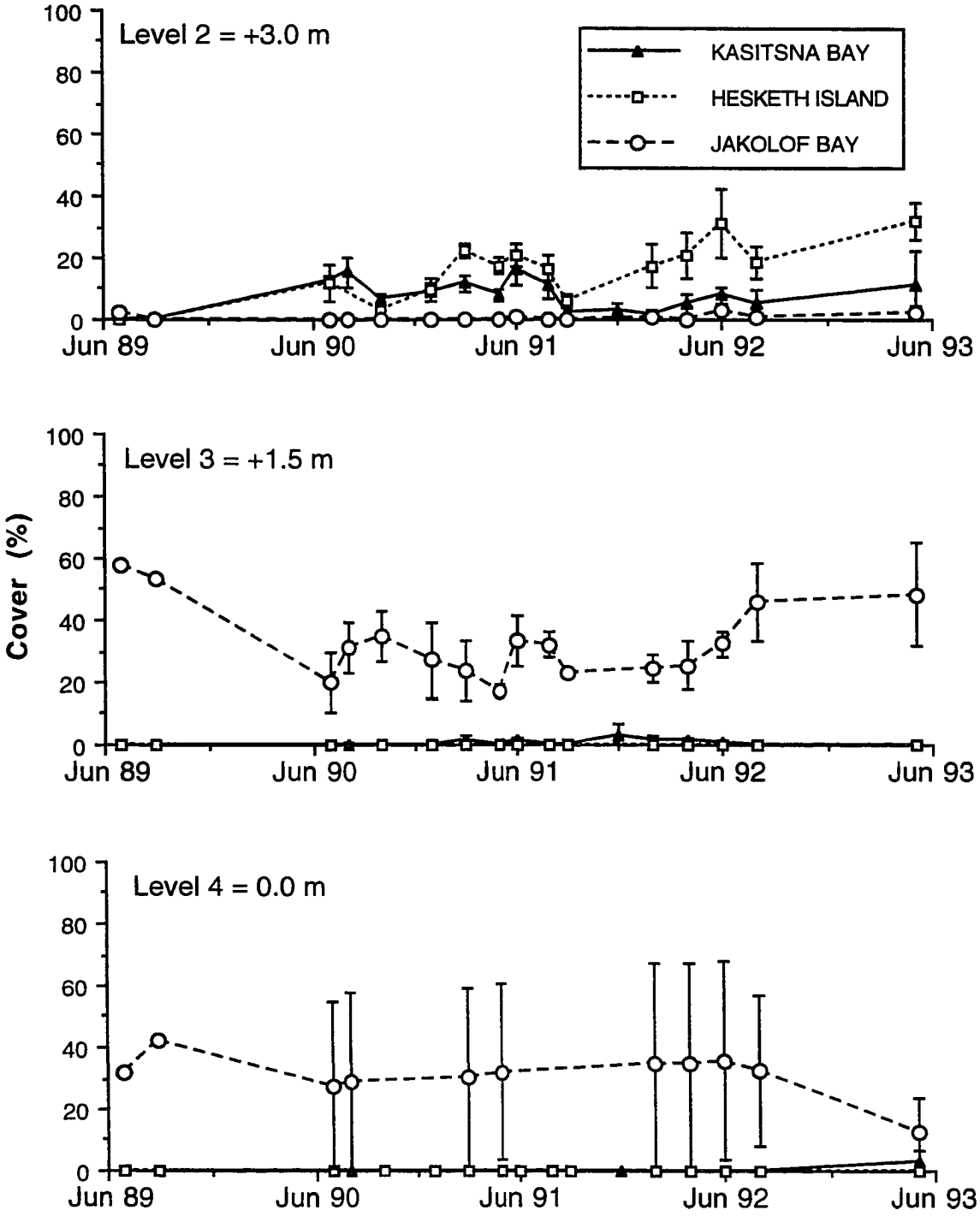

Figure 3.5: Mean cover (%±SE) of the mussel *Mytilus trossulus* at 3 sites in Kachemak Bay. Relative exposure of sites to wave action is Hesketh Island > Kasitsna Bay > Jakolof Bay.

At Jakolof Bay, mussel cover was 30-40% in levels 3 and 4 and persisted throughout the course of this study until the winter of 1992-1993, when a marked decline in level 4 occurred. However, neither of the two sites exposed to higher wave action showed any mussel cover below the level 2. Mussels showed recruitment pulses each summer, but cover then returned to low levels (Fig. 3.5). The temporal pattern of small recruitment pulses followed by a decrease in abundance of similar magnitude occurred in level 3 at Jakolof Bay and level 2 at Kasitsna Bay and Hesketh Island. Mussel cover at Jakolof Bay tended to be greatest lower in the intertidal and higher overall than at exposed sites.

MACROALGAE: Most species in this group are annuals (Dethier & Duggins, 1988) or act as annuals in Alaska (Dames & Moore, 1977), and lose most of their biomass in the winter months. This group exhibited a distinct seasonal pattern with minimum cover during winter and maximum cover in July and August (Fig. 3.6). This pattern is especially pronounced in level 4, where the cover of kelps varied up to 80% between summer and winter.

Macroalgal cover at Jakolof Bay, the most protected site, was consistently lower than other sites at all tidal levels. This was in contrast to the restricted mouth of Jakolof Bay (<1 km from the study site) which seasonally supported extensive *Alaria fistulosa, Laminaria groenlandica*, and *Nereocystis luetkeana* populations (Dames & Moore, 1977; personal observation).

CARIOSUS: The thatched barnacle, *Semibalanus cariosus*, is considered separately because its distribution was distinctly lower in the intertidal than the other barnacles. Also, its morphology and associations/interactions are distinctive compared to the other barnacles. *S. cariosus* generally had a

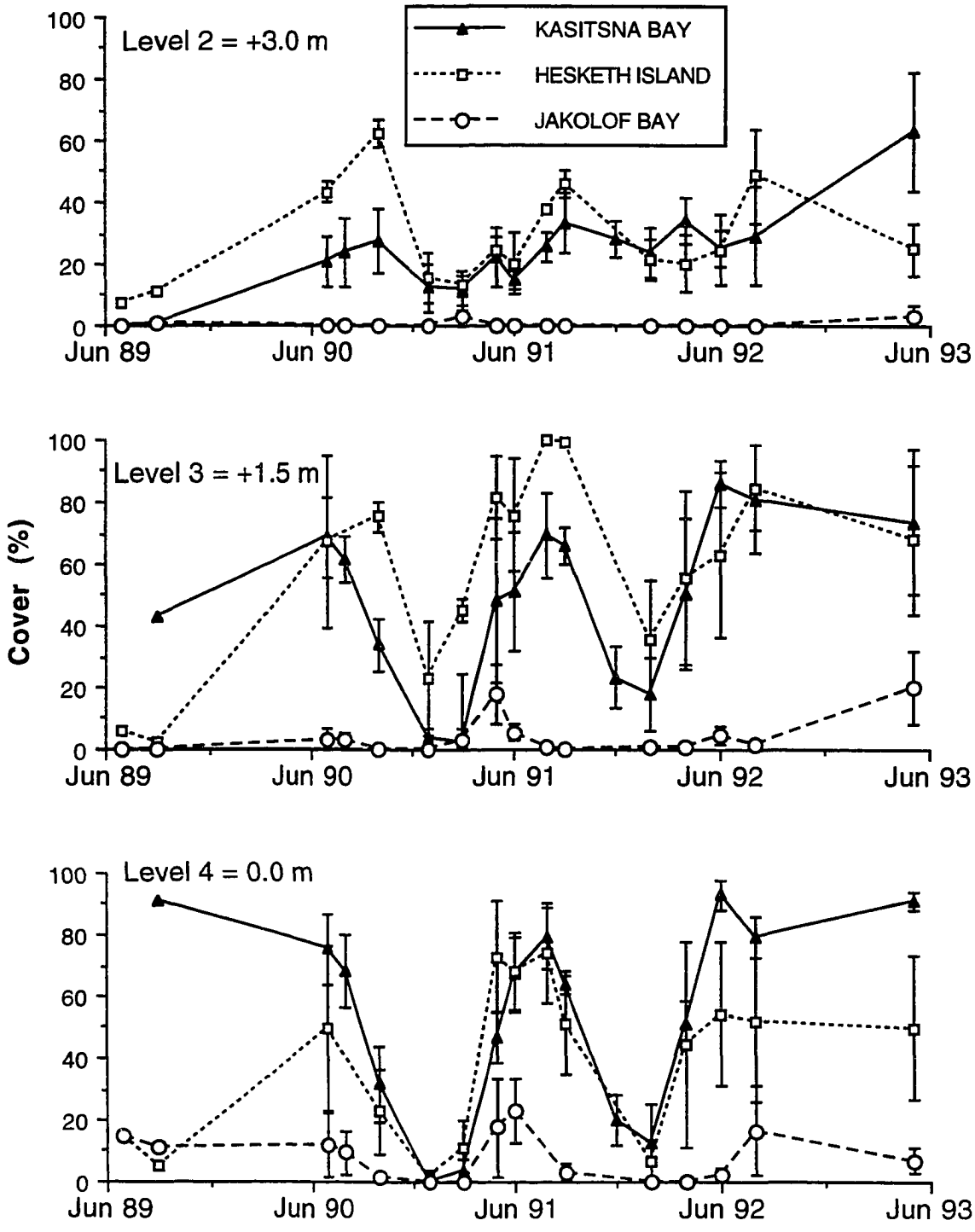

Figure 3.6: Mean cover (%±SE) of the macroalgae at 3 sites in Kachemak Bay. Relative exposure of sites to wave action is Hesketh Island > Kasitsna Bay > Jakolof Bay.

vertical distribution in the intertidal similar to the macroalgal group. Cover data are, therefore, inversely related to the seasonal variability of the macroalgae because the sampling methodology was not sensitive to understory species (Fig. 3.7). As a result, trends in *S. cariosus* cover determined by examining data from winter censuses when macroalgae were minimal. Cover of *S. cariosus* in winter indicate that this barnacle has relatively constant year-to-year cover. This species occupied more space in the lowest intertidal zone (level 4), and displayed no major yearly increases or decreases during the term of this study.

TOTAL COVER: Seasonal variation in total cover, the sum of all cover groups, was less pronounced at all intertidal levels at Jakolof Bay than either of the two sites more exposed to wave action (Fig. 3.8). The consistently high cover in the upper intertidal (levels1 and 2) at Jakolof Bay in the latter 2 years study resulted from a monoculture of *Fucus gardneri*. Seasonal shifts in total cover are evident at both Kasitsna Bay and Hesketh Island, with the greatest seasonal variations occurring at the lowest tide level due to the seasonal variation in the macroalgae. Even with the large seasonal fluctuations, cover was generally >50% year-round at most sites with cover during summer often exceeding 80%.

Little Tutka Bay

Little Tutka Bay is a small pocket bay that has both rocky and soft bottom habitats. The entrance to the bay is through a winding, narrow channel which is subject to very strong currents. Although rocky habitats occur at Little Tutka, the substrate consists primarily of jagged cobble-sized rocks and

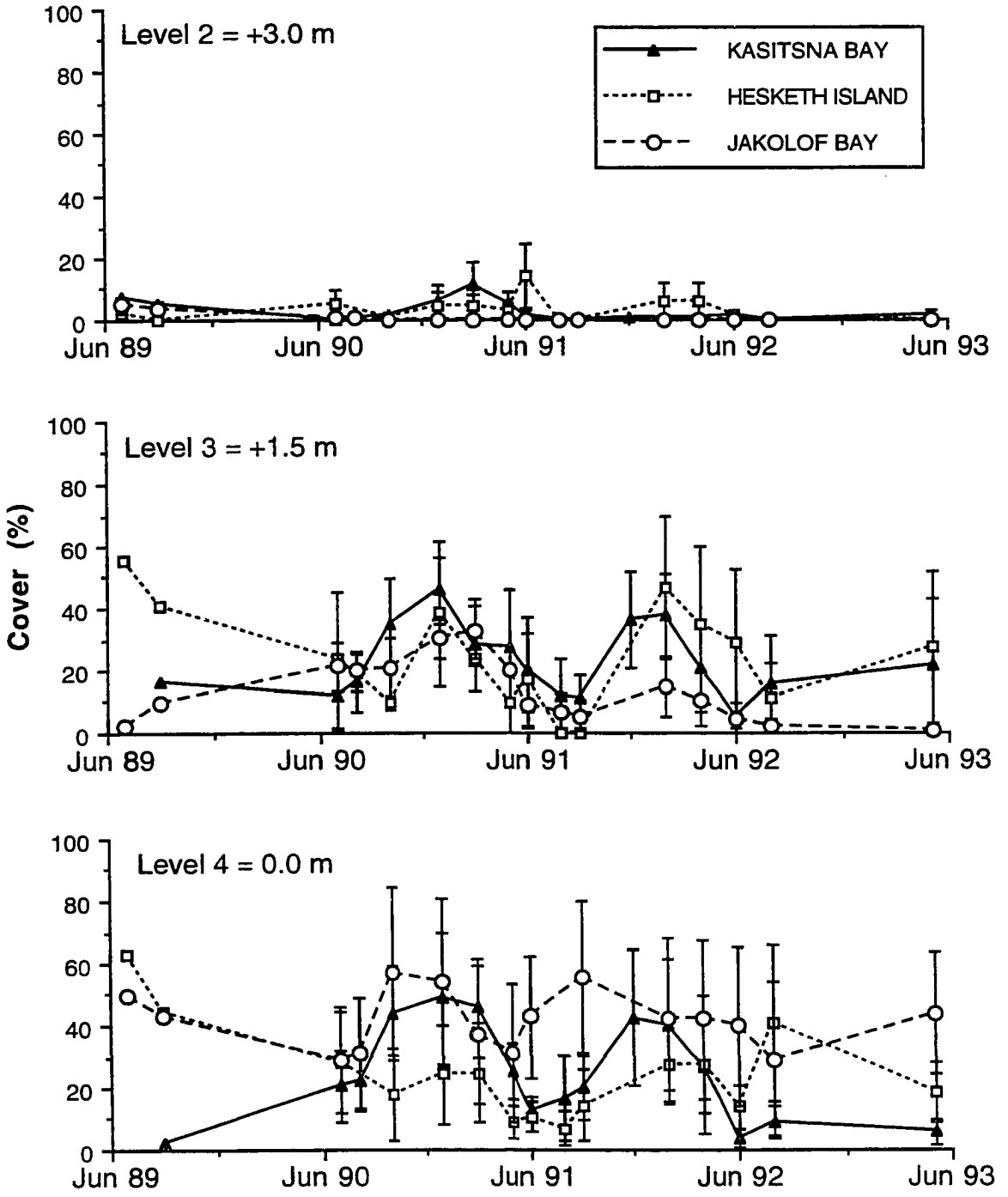

Figure 3.7: Mean cover (%±SE) of the barnacle *Semibalanus cariosus* at 3 sites in Kachemak Bay. Relative exposure of sites to wave action is Hesketh Island > Kasitsna Bay > Jakolof Bay.

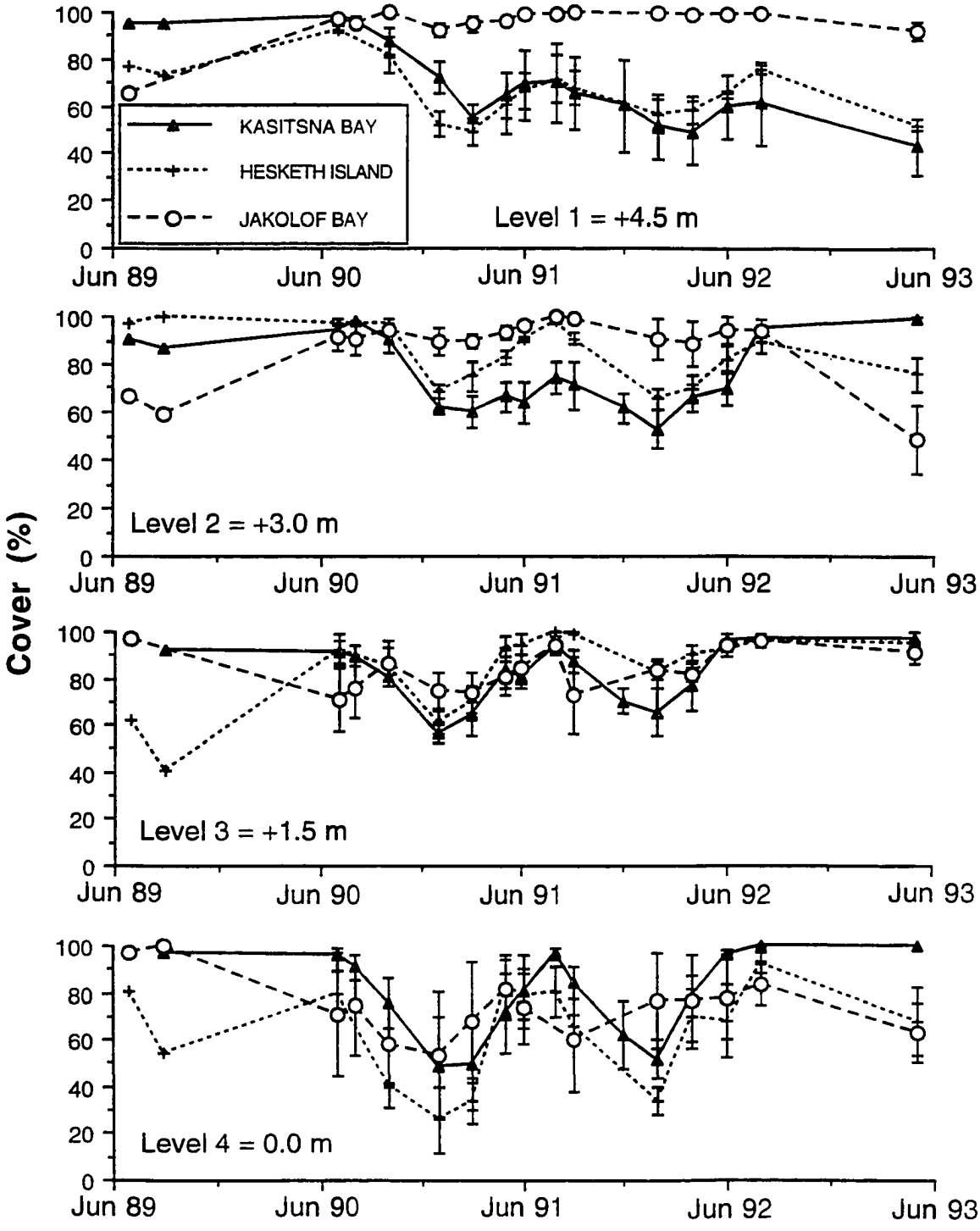

Figure 3.8: Mean cover (%±SE) of all groups at 3 sites in Kachemak Bay. Relative exposure of sites to wave action is Hesketh Island > Kasitsna Bay > Jakolof Bay.

precluded establishment of more than one transect line. At level 1, barnacles were the only group observed and remained relatively constant during the study (Fig. 3.9), until the winter of 1992-1993 when barnacle cover dropped precipitously, leaving the surface of the quadrat almost completely empty.

At level 2 (Fig. 3.9), barnacles were relatively abundant but occupied less space than at level 1. Barnacles exhibited a slow, but steadily increasing trend from September 1989 until May 1993. A small aggregation of mussels persisted at this level throughout the study. *Fucus* was absent in the quadrat until June 1993, and then increased to about 40% cover by August 1992 and 65% by May 1993, replacing barnacles as the most prevalent organism in the at level 2.

The quadrat at level 3 initially was almost totally empty (Fig. 3.9). Empty tests and large piles of shell hash at the base of the quadrat indicated that *S. cariosus* and mussels had previously occupied the quadrat, but were likely killed by the 1989 freeze (personal observation). High-shore barnacles (not *S. cariosus*) recruited each year but did not persist until July 1992. As in level 2, *Fucus* cover was minimal until June 1992 when rapidly increased to >80% cover, utilizing space previously occupied by barnacles.

The quadrat at level 4 initially was dominated by an extensive mussel bed. By early 1991, a steady decline began. Initially, mussels were partially replaced by *S. cariosus,* but there was also a significant amount of free space. In 1991, macroalgae colonized the quadrat and subsequently dominated cover.

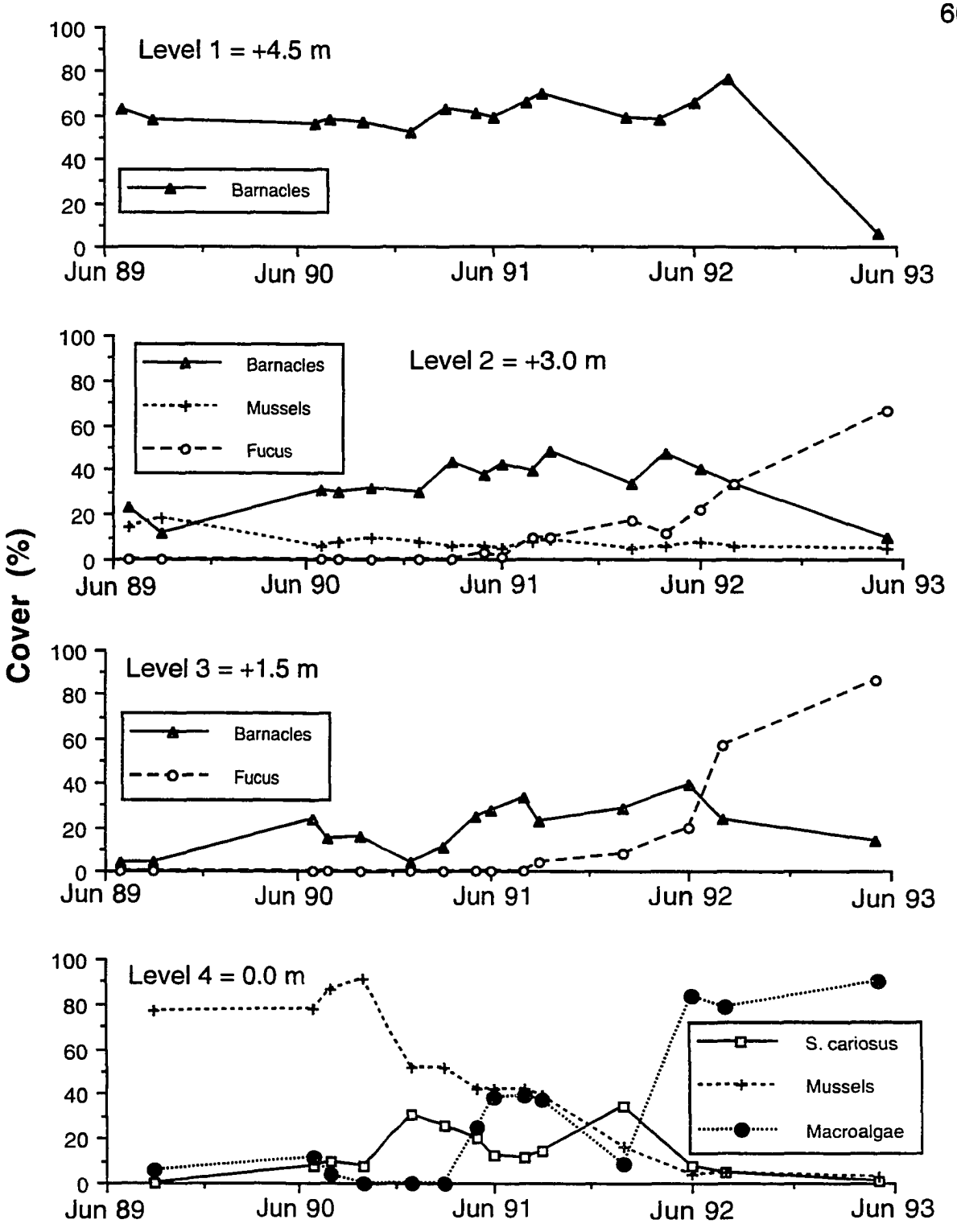

Figure 3.9: Cover (%) of major groups at 4 tide levels at Little Tutka Bay (n=1 quadrat per level).

Seasonal Variations in Cover

Analysis of seasonal variation was conducted to determine which cover groups varied significantly between summer and winter. An additional goal of this analysis was to identify which groups were most responsible for the seasonal variations in total cover. Cover data from the first summer (1989), however, were eliminated from this analysis because of the likelihood that the freeze in January 1989 resulted in aberrations in patterns of abundance during that summer. Cover of most groups stabilized after approximately 12 months (see next section on successional trends). Data from Little Tutka Bay were not included because of the lack of replication at that site.

Analysis of summer-winter trends in cover indicates the greatest variation in total cover at the lower intertidal levels at all sites and the least variation at the most protected site (Table 3.1). There was no significant seasonal variation in total cover at any of the sites in level 1, and the most protected site (Jakolof Bay) had relatively constant total cover at all intertidal levels. Trends in total cover at all sites combined (Table 3.1; final column) indicate that seasonal differences increased from with decreasing tidal height, with the greatest variation at the two lowest tide levels.

The seasonal variation in total cover was primarily due to variation in macroalgal abundance. At level 2, *Fucus* varied significantly at the two most exposed sites despite its high absolute abundance and its perennial life history. Short day length, increased wave action due to storms, and low temperatures probably all contributed to the reduced *Fucus* cover in winter.

At the most exposed site (Hesketh Island), barnacle cover also varied seasonally in the upper-mid intertidal. As the increase in barnacle cover

Table 3.1: Seasonal variation in cover (%) of major groups in relation to tide level at 3 locations in Kachemak Bay. Summer is April - September and winter is October - March. P-values result from one-way analysis of variance after subjecting data to an arcsine-square root transformation to conform to assumptions of parametric statistics. Significance levels are: <0.05=*, <0.01=**, <0.001=***, and <0.0001=****. The overall P-value column results from comparison of seasonal variation in cover groups by combining all sites.

TIDE LEVEL	COVER GROUP	Hesketh Island (exposed)				Kasitsna Bay (moderate exposure)				Jakolof Bay (protected)				ALL SITES
		Summer	Winter	% Chng	P-val	Summer	Winter	% Chng	P-val	Summer	Winter	% Chng	P-val	P-VALUE
Level 1	barnacle	18.9	20.9	+2.0	.85	27.2	26.4	-0.8	.99	9.0	11.6	+2.6	.32	.51
+4.5 m	*Fucus*	48.3	37.3	-9.0	.10	39.7	32.1	-7.6	.36	88.9	85.1	-3.8	.39	.19
	mussel	0.3	0.3	0	.86	0.2	1.0	+0.8	.19	0	0	0	----	.26
	S. cariosus	0	0	0	----	0	0	0	----	0	0	0	----	----
	oth. algae	2.3	1.2	-1.1	.22	1.6	0.8	-0.8	.51	0	0	0	----	.24
	TOTAL	69.8	59.7	-10.1	.09	68.8	60.3	-8.5	.25	97.9	96.8	-1.1	.67	.19
Level 2	barnacle	6.1	17.1	+11.0	**	10.9	13.5	+2.6	.47	25.9	39.4	+13.8	.12	*
+3.0 m	*Fucus*	26.8	13.6	-13.2	***	31.0	20.7	-10.3	**	67.0	50.4	-16.6	.13	**
	mussel	18.4	12.8	-5.6	.14	9.3	6.4	-2.9	.19	0.5	0.2	-0.3	.65	.23
	S. cariosus	2.2	3.6	+1.4	.51	1.0	3.9	+2.9	.06	0.1	0	-0.1	.34	.09
	oth. algae	34.2	28.1	-6.1	.26	25.4	20.6	-4.8	.29	0	0.9	+0.9	.14	.60
	TOTAL	87.7	75.3	-12.4	*	77.7	65.0	-12.7	*	93.6	90.8	-2.8	.25	**
Level 3	barnacle	1.4	0	-1.4	.53	0.2	0	-0.2	.12	9.8	11.7	+1.9	.61	.85
+1.5 m	*Fucus*	0.8	0.4	-0.4	.77	8.1	8.4	+0.3	.65	29.8	15.5	-14.3	.07	.47
	mussel	0	0	0	----	0.3	1.3	+1.0	.20	29.5	27.0	-2.5	.66	.98
	S. cariosus	15.9	31.3	+15.4	.06	15.4	36.2	+20.8	**	10.9	25.0	+14.1	**	****
	oth. algae	76.3	43.8	-32.5	*	64.4	20.9	-43.5	****	3.6	1.0	-2.6	.09	***
	TOTAL	94.4	75.6	-18.8	****	88.4	66.9	-21.5	****	83.5	80.3	-3.2	.28	****
Level 4	barnacle	1.7	0	-1.7	.36	0.2	0	-0.2	.29	0.7	0	-0.7	.25	.09
0.0 m	*Fucus*	0	0	0	----	1.5	0	-1.5	.24	0.4	0	-0.4	.24	.12
	mussel	0	0	0	----	1.9	0	-1.9	.47	26.9	19.5	-7.4	.53	.44
	S. cariosus	17.4	23.7	6.3	.41	15.5	47.3	+31.8	****	36.3	45.8	+9.5	.43	**
	oth. algae	58.5	10.2	-48.3	***	67.5	11.9	-55.6	****	11.1	0.2	-10.9	*	****
	TOTAL	77.7	33.9	-43.8	****	86.6	59.2	-27.4	****	75.5	65.5	-10.0	.43	****

(11%) was similar to the decrease in *Fucus* cover (13%), this pattern was probably a result of incomplete census of barnacles under *Fucus* when the canopy is dense.

In the lower two levels, much of the seasonal variation in cover was due to the influence of the macroalgae which regress in the winter due to blade loss. Consequently, the low-intertidal macroalgae exhibited extreme seasonal cycles in area covered with macroalgal cover varying as much as six-fold between summer and winter. Similar to the *Fucus*-barnacle interaction at higher intertidal levels, variation in *S. cariosus* cover was primarily a result of its occurrence under the algal canopy in the summer.

Successional Trends

The severe freeze in January 1989 presented an opportunity to examine how rocky intertidal communities in this region recover from stochastic disturbance events. Cover data from the permanent quadrats were analyzed to determine the ways in which composition of the community changed from an initial census only a few months following the freeze to a census in August 1992.

A tremendous amount of free space was evident during the spring following the freeze as shells of dead organisms were washed from the rocks (personal observation). Most of the free space was filled by a heavy barnacle settlement during the spring of 1989. When the permanent quadrats were established in July 1989, barnacle recruits monopolized much of the upper

intertidal (Fig. 3.3). The barnacle set was considered the first stage of the recolonization sequence and the starting point of community succession. Of course, rock surfaces were undoubtedly first colonized by bacteria and microalgae (e.g. diatoms), but those processes are not within the context of this analysis as the focus of this paper is on factors affecting macro-organisms. Seasonal cycles likely do not affect the results because censuses used in this analysis occurred at the same time of year – during the summer cover maximum.

Analysis (Table 3.2) indicate that upper-shore barnacle cover decreased dramatically at all levels where it occurred. Barnacles lost >50% cover from initial values, and final barnacle cover was only 19%, 7%, and 0% of initial cover values in the upper three levels, respectively. Additionally, barnacle vertical distribution contracted (Fig. 3.3). In July 1989, barnacles were found in the upper three tide levels at some sites but disappeared from the level 3 before the August 1992 census. Barnacles were replaced by *Fucus* in the upper two levels, with the magnitude of *Fucus* increase similar to the decrease in barnacle cover. Other species replacements did not occur. Total cover did not change significantly from July 1989 to August 1992 except at the level 3. This was primarily due to an increase in macroalgal cover, despite the non-significant result.

Table 3.2: Change in cover (%) of major groups and total cover from July 1989 (initial) to August 1992 (final). Total cover may differ from the sum of the listed cover groups because those groups with low abundance were omitted. F-ratios and P-values result from one-way analysis of variance. Raw cover data were arcsine-square root transformed prior to analysis.

TIDE LEVEL	COVER TYPE	INITIAL COVER MEAN (SE) N=3	FINAL COVER MEAN (SE) N=9	F RATIO	P VALUE
Level 1	Barnacle	65.33 (6.17)	12.56 (3.84)	20.06	0.0012
+4.5 m	*Fucus*	12.00 (5.00)	65.33 (11.03)	5.91	0.0353
	Total	77.33 (8.65)	78.89 (7.18)	0.16	0.7014
Level 2	Barnacle	71.33 (11.25)	5.33 (3.55)	40.79	0.0001
+3.0 m	*Fucus*	2.33 (0.88)	53.67 (11.35)	7.39	0.0216
	Mussel	0	7.89 (3.33)	2.73	0.1297
	Total	81.00 (13.05)	92.78 (2.41)	0.92	0.3608
Level 3	Barnacle	17.33 (6.56)	0	87.69	0.0001
+1.5 m	*Fucus*	12.00 (10.53)	16.22 (8.64)	0	0.9853
	Mussel	18.00 (18.00)	15.22 (8.46)	0.01	0.9147
	S. cariosus	8.67 (3.52)	10.00 (5.83)	0.21	0.6602
	Macroalgae	15.00 (14.01)	54.89 (15.09)	1.65	0.2284
	Total	71.00 (13.42)	96.33 (1.09)	14.17	0.0037
Level 4	*S. cariosus*	15.00 (14.01)	26.11 (11.31)	0.27	0.6147
0.0 m	Macroalgae	35.67 (27.72)	51.44 (12.02)	0.30	0.5980
	Total	80.67 (15.85)	92.00 (3.82)	1.13	0.3132

Discussion

The multi-year temporal scale on which this study was conducted revealed seasonal cycles and inter-annual changes of species cover in this community that could not have been elucidated by a short-term study. The unusually severe freeze in January 1989 also provided an opportunity to observe the response of the community as it recovered from a stochastic disturbance event. No data are available for these sites documenting distribution and abundance patterns of intertidal organisms before the freeze, so quantification of the effect of the freeze on intertidal organisms is impossible. However, photographs taken and observations made during in April and June 1989 revealed evidence of extensive mortality of many intertidal species. Observations included large intact beds of mussels, with virtually all individuals dead with shells gaping, and no evidence of predation. Later, extensive windrows containing thousands of mussel shells were common on beaches; an event which has not been observed in the ensuing 4 years. Additionally, large stands of empty high-shore barnacle tests were common, as well as large empty spaces of rock, immediately below which were large heaps of barnacle shell hash. The same observations were noted in the low intertidal with very large *S. cariosus* shells, indicating that the effects of the freeze extended into the low intertidal as well. Hence, although the direct impacts of the freeze cannot be quantified, there is evidence that its effects were widespread.

Initially, the upper intertidal community was spatially dominated by high-shore barnacles. The high coverage of barnacles evident at the beginning of

this study resulted from early colonization of extensive free space presumably made available by winter mortality of resident organisms. Dominance by barnacles was short-lived, however, as *Fucus* recruited into the high-shore zone and gained spatial dominance within 2 years in most cases. At the lowest level of *Fucus*' intertidal distribution, however, initial recruitment success was delayed by 2 years at Jakolof Bay. The reason *Fucus* did not increase in cover at the lower mid-level for almost two years is unknown, but could be explained by its mode of recruitment.

Fucus eggs have little dispersal ability, and usually attach quite close to their parent plant (Burrows & Lodge, 1950; Sousa, 1984; Hoffman, 1987; Arrontes, 1993). Further, *Fucus* eggs are negatively buoyant and thus have a tendency to sink (McLachlan *et al.*, 1971; Lobban *et al.*, 1985). Therefore, successful colonization of the lower intertidal may have been dependent upon an abundant population of mature, reproductive plants in the immediate vicinity higher on the shore. As *Fucus* did not fully recover at upper shore levels for almost two years (Fig. 3.4), there would have been few mature plants and therefore a potential scarcity of propagules for colonization of lower levels.

Mussels were also an apparent victim of the 1989 freeze and initially exhibited virtually no coverage of intertidal substrate. Mussels are considered to be a dominant competitor for space in the intertidal (Seed, 1976; Menge, 1976; Lubchenco & Menge, 1978), and an increase in mussel cover was expected. Mussels recruited each year, but cover did not increase following recruitment or even persist. Investigation of trophic interactions

revealed that *M. trossulus* abundance was controlled by predation by the gastropod *Nucella lima* (Chapter 5).

In the low intertidal, macroalgae exhibited a distinct seasonal pattern with large swings in abundance from high summer cover to low winter values. The pronounced high-latitude seasonality in Kachemak Bay has caused differences in the seasonal patterns of macrophyte abundance and has resulted in different mechanisms of population regulation compared to temperate latitudes on the west coast. In Washington, most of the macroalgal species low in the intertidal are perennial, and populations are regulated by herbivores, principally the chiton *Katharina tunicata*. In Alaska, however, physical factors associated with seasonal extremes (e.g. light) regulate macroalgal abundance, and therefore macrophyte cover is decoupled from herbivore control, even though *Katharina* abundance in Alaska is similar to Washington (Dethier & Duggins, 1988).

In general, species vertical distributions and cover at Jakolof Bay consistently differed from the two sites which were more exposed to wave action and which generally exhibited similar patterns of species abundance and distribution. At Jakolof Bay, barnacle cover exhibited a greater vertical range, *Fucus* cover was greater at all intertidal levels (repeated measures ANOVA: df=1,8; F_{RM}=9.11; P=0.0166) and extended over a greater vertical range than at the other sites, mussels were found in greater abundance (repeated measures ANOVA: df=1,6; F_{RM}=13.74; P=0.0100), and the zones of greatest mussel cover were distinctly lower than the other two sites. Additionally, macrophytes were significantly less abundant at Jakolof Bay

compared to other sites (repeated measures ANOVA: df=1,10; F_{RM}=24.09; P=0.0006).

Although the mechanisms underlying these distributional differences were not experimentally investigated, it is possible that the local water motion regime be important in maintaining this pattern. The Jakolof Bay study site is located inside an embayment very protected from wave action. However, the high tidal range in the region (up to 9-10 m) combined with the shallow and constricted entrance to Jakolof Bay results in tidal currents of 2-3 knots during spring tides (Dames & Moore, 1977). Although such currents may not be as great at the study site which is 1 km from the bay entrance, the quadrats are located on a prominent outcropping which extends into the middle of the bay, and is subject to swift currents during ebb and flood tides (personal observation).

The low wave energy, high-velocity tidal current regime may be important in species distributions. Lack of wave action can benefit sessile species such as mussels by eliminating wave-caused mortality which can remove large patches of mussels which are often attached to each other by byssal threads (Paine & Levin, 1981; Lubchenco & Menge, 1978). On the other hand, diminishing environmental harshness (Hughes, 1980) in the form of decreasing wave action can facilitate predator control of prey by allowing predators to forage and attack prey more effectively (Menge 1976, 1978a, b, 1983; Menge & Lubchenco, 1981). High current velocities would also benefit sessile filter feeders by increasing food availability.

Data from Little Tutka Bay indicate that ecological processes operate on different temporal scales, as changes in species cover occurred more slowly

than at the other sites. Established species, except for *Fucus* and the other macrophytes in the latter months of the study, generally increased their space occupation rather slowly through growth. Moreover, recruitment processes seem to be dampened compared to other sites. Free space took longer to be colonized, and the magnitude and predictability of recruitment of all groups observed at this site was typically lower than observed elsewhere.

The low rate and predictability of recruitment processes may possibly be explained by the physical characteristics of the Bay. Compared to Jakolof Bay, Little Tutka has a greater proportion of soft bottom habitats, and the hard substrate that exists is primarily composed of small cobbles. The result is a much smaller potential source population of resident adults. This factor is probably more important for *Fucus,* which is a poor disperser, than for barnacles and mussels, whose larvae spend several weeks in the plankton. Furthermore, the bay almost completely empties of water during spring low tides. Thus, planktonic propagules of benthic adults are necessarily carried out of the bay. Hence, populations in Little Tutka may be limited by larval availability.

The rockweed, *Fucus gardneri*, is an important component of the intertidal community. In general, *Fucus* was rare at the initiation of this study (<10% cover). Once *Fucus* recruited, its abundance increased and it rapidly covered or displaced other organisms. As a result, from 1991-1993, *Fucus* was a dominant occupant of space at upper levels of undisturbed intertidal rocky areas around Kachemak Bay, achieving high densities over a greater vertical range than most other species. The data suggest *Fucus* is most successful in habitats with good water motion but sheltered from waves.

Despite the spatial dominance in the upper zones in the latter 2 years of this study, it often took an extended time for *Fucus* to become established. Two possible non-exclusive explanations seem to fit the observed patterns.

The first involves the limited dispersal ability of *Fucus* propagules. *Fucus* eggs are comparatively heavy and sink rapidly (McLachlan *et al.*, 1971; Lobban *et al.*, 1985). Additionally, *Fucus* eggs are released from the parent receptacle within a thick mucilage medium that facilitates attachment to surfaces (Lobban *et al.*, 1985; Chapter 6, this study). The result of these factors is rapid settling of *Fucus* zygotes and a limited dispersal distance (cms) (Burrows & Lodge, 1950; Sousa, 1984; Hoffman, 1987; Arrontes, 1993) and a difficulty colonizing new habitats even moderate distances away from an established parent population.

The second possible explanation for the delayed initial *Fucus* colonization involves chemical defenses against herbivore grazing (reviewed by Hay & Fenical, 1988). *Fucus spp.* adults are relatively unpalatable to herbivores because of the presence of large quantities of phenolic compounds (Steinberg, 1985; Ragan & Glombitza, 1986; Van Alstyne, 1988a, b). It is not known whether *Fucus gardneri* germlings produce such compounds, but Lubchenco (1983) demonstrated that younger, smaller *Fucus vesiculosus* plants in New England were much more palatable to herbivores than large plants. The difference in palatability of the two sizes of *F. vesiculosus* could be attributed to higher concentrations of phenolic compounds in adult plants (Denton *et al.*, 1990). The effect of herbivore grazing before germlings reach a refuge size of about 3 cm frond length (Lubchenco, 1983) can play a role in limiting the establishment of *Fucus* populations in areas where they recruit.

Regarding successional changes to the community, it appears that the high initial cover and large vertical distribution of barnacles was part of a successional sequence where barnacles replaced by *Fucus* at the upper tidal levels. Barnacle cover enhances establishment of several intertidal species such as the mussels *Mytilus edulis* (Suchanek, 1986) and *Brachiodontes semilaevis* (Lively & Raimondi, 1987; Lively *et al.* 1993), *Fucus spp.* (Hawkins, 1981; Lubchenco, 1980, 1983; Chapter 6, this study) and other macroalgae (Jernakoff, 1983). The observed heavy barnacle settlement may facilitate succession (Connell & Slayter, 1977) in this community, as barnacle cover was a first step in the community's recovery from disturbance. Despite the successional sequence that shifts from barnacle to *Fucus* dominance, barnacles were not completely eliminated from the intertidal. They persisted at low cover levels in the *Fucus* understory and occupied patches where *Fucus* did not to colonize.

The presence of barnacles enhances the establishment of *Fucus* populations, possibly by increasing surface heterogeneity and thereby providing grazing-free refuges for *Fucus* germlings (Burrows & Lodge, 1950; Choat, 1977; J.L. Menge, 1975; Lubchenco & B.A. Menge, 1978; Lubchenco, 1980, 1983; Hawkins, 1981; Norton & Fetter, 1981; Jernakoff, 1983; but see Chapman, 1989; Chapter 6, this study). Once *Fucus* becomes established, it can benefit barnacle populations by reducing temperature extremes and the potential for desiccation. At high *Fucus* densities, the interaction between *Fucus* and barnacles may become negative. Holdfasts may overgrow barnacles tests, resulting in the smothering of barnacles, and heavy *Fucus* cover dampens water motion, reducing food availability to barnacles (Moore,

1934; Burrows & Lodge, 1950; Dayton, 1973; Southward & Southward, 1978; Jernakoff, 1983; Jernakoff, 1986).

The latter scenario seems to have occurred in this study as the establishment of extensive *Fucus* stands coincided with a substantial decrease in barnacle cover. Two observations argue against the possibility that *Fucus* simply occupied space vacated by barnacles. First, the *Fucus* increase occurred while barnacle cover was at or near its maximum (Fig. 3.3, 2.4). Second, many *Fucus* holdfasts were attached to barnacle tests rather than to bare rock surface (personal observation).

The intertidal community in Kachemak Bay might seem, based on short-term observations, to be an extremely variable, and hence unstable community. A field study of only a few months would reveal population abundances that are constantly in flux with no discernible pattern. However, the longer-term observations (4 years) of this study reveal recurring and predictable patterns of species cover and therefore can provide insight into the mechanisms responsible for the dynamics of this community.

Perhaps the most striking aspect of this community is its distinct seasonality. The pronounced variation of physical factors such as temperature and photoperiod at such a high latitude result in an intertidal community whose characteristics change dramatically between summer and winter.

Despite the significant effect of seasonal extremes in Kachemak Bay and the resulting distinct seasonality of intertidal populations, the community seemed in general to be quite stable over comparatively longer time periods. The freeze clearly impacted some cover groups. Barnacles (both high- and

low-shore) and mussels all suffered severe losses as seen by the presence of large numbers of empty shells both on and washed from rocks soon after the freeze. The scarcity of *Fucus* during the summer following the freeze (1989) and subsequent dominance at several sites and tide levels suggest that it may have also been affected by the freeze. Even species lower in the intertidal may have been affected. Most species exhibited lower cover in 1989 at their upper vertical limit than where they occurred at lower tide levels. These differences subsequently disappeared, indicating recovery at species' upper levels. Most populations, with the exception of mussels (Chapter 5), recovered from the freeze within 2 years (Fig. 3.3). Successional processes did not seem to dominate the community, as only one major species replacement occurred during the course of this study. Most species re-occupied zones where they likely occurred before the freeze.

In summary, the intertidal community in Kachemak Bay is dynamic, with constantly changing abundances of species in relation to each other, and to the environment. Superimposed on these variations are recurring and predictable patterns that become apparent only when the community is examined on an appropriate time scale.

SUMMARY

Temporal and spatial trends in cover were assessed in field experiments from 1989-1993 for several groups of intertidal space-occupying including upper-shore barnacles, the rockweed *Fucus gardneri*, mussels, lower-shore barnacles, and a guild of macroalgae prevalent in the lower intertidal.

Quadrats spanned a vertical range of 4.5 m, and temporal patterns of species' distributions and abundances were assessed separately at sites along a gradient of exposure to wave action.

Initially, barnacles dominated upper- and mid-level shorelines. This resulted from extremely heavy barnacle settlement which filled essentially all space made available by freeze-induced mortality. Barnacles were eventually replaced by *Fucus gardneri*, which became the dominant space occupant in the upper intertidal after approximately 2 years. In the mid-intertidal, mussels (*Mytilus trossulus*) recruited after the freeze, but failed to significantly increase their cover over the course of the study. In the lower intertidal zone, macrophytes exhibited extreme seasonality; they dominated space in the summer, but cover was minimal in winter . The barnacle, *Semibalanus cariosus*, exhibited relatively little variation in abundance over the term of this study, and was the principal space occupying species in the low intertidal when macroalgal species were scarce. There were differences in species abundances and distributions at protected sites in comparison to sites more exposed to wave action. At protected sites, *Fucus* achieved higher overall cover and occupied a greater vertical range, while mussels occurred at lower intertidal levels. Additionally, macroalgal cover was relatively scarce in the low intertidal at protected sites.

This study demonstrates the increased influence of physical forcing functions at high latitudes. The distinct seasonal cycles in the biological characteristics of the intertidal community are clearly linked to seasonality of environmental parameters apparent in Kachemak Bay.

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CHAPTER 4

ROLE OF RECRUITMENT IN REGULATING INTERTIDAL BARNACLE POPULATION DYNAMICS

INTRODUCTION

A principal goal of ecological research is to understand the factors that determine local patterns in the distribution and abundance of populations, as the processes which regulate local populations exert considerable influence on community structure. Field experimentation in the rocky intertidal has traditionally focused on adults as they interacted, resulting in a large body of work documenting the importance of factors such as predation, competition, and physical disturbance in the dynamics of intertidal populations and community structure (e.g. Connell, 1961, 1970; Paine, 1966, 1974; Dayton, 1971; Menge, 1976; Menge & Sutherland, 1976; Sousa, 1979; Dethier & Duggins, 1984; Palmer, 1984; Wethey, 1984a; Bertness, 1989). Ultimately, the results of studies such as these were generalized beyond the habitats and spatial scales in which they were conducted.

Important as they are to the understanding of ecological processes controlling community structure, the adult-interaction paradigms ignore a key component of the life cycle of benthic marine invertebrates. Most species have a multi-phasic life cycle (Grosberg & Levitan, 1992) in which larvae spend a portion of their life as plankton before colonizing the benthos (Fig. 4.1). Larval dispersal is the only means by which sessile or sedentary benthic species can colonize habitats away from adult populations, minimizing the risk of local extinction and maximizing gene flow (Strathmann, 1974). During residence in the water column larvae are subjected to different mortality sources and regulatory processes than sessile adults (Dayton, 1984). Recruitment is the link between the planktonic larval and benthic adult components of these life-cycles (Fig. 4.1) and can act as a filter between life-

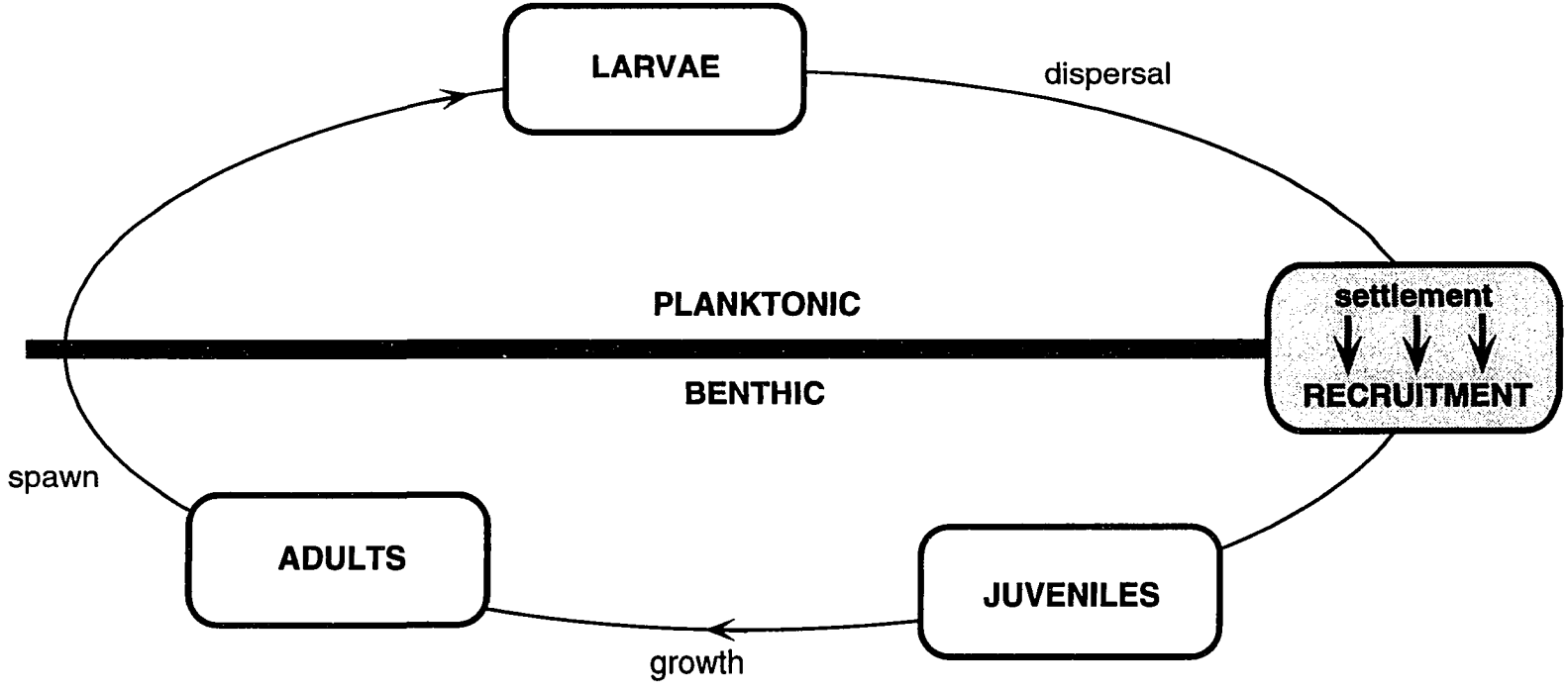


Figure 4.1: Generalized life cycle of a benthic marine invertebrate with planktotrophic larvae.

history stages. Consequently, variations in recruitment may influence the population dynamics of a species and, ultimately, community structure (Underwood & Denly, 1984; Lewin, 1986; Roughgarden, *et al.,* 1988).

The term recruitment is generally considered to mean the appearance of the smallest recognizable individual in a benthic habitat (Connell, 1985; Cameron, 1986). Consequently, recruitment includes both settlement processes and survival of settlers. The length of time from settlement to recruitment can range from hours to months (Scheltema, 1974) and reflects the limitations of the observer rather than the biology of the organism. Thus, observed patterns of recruitment may result from either differential settlement processes or differential survival during that interim period (Keough & Downes, 1982).

Thorson (1950) noted that species with a life-cycle that includes a planktonic dispersal phase exhibit greater population fluctuations than otherwise similar non-planktonic species. Larger population fluctuations were attributed to the decoupling of local production of propagules from local recruitment via the planktonic larval stage and the variable supply of larvae to a particular site. These ideas are encompassed in the 'supply-side ecology' paradigm (Lewin, 1986; Underwood & Fairweather, 1989; Hughes, 1990).

Recruitment regulation of a population can occur when the number of recruits is not great enough to saturate the spatial resource. At low recruitment levels, mortality of recruits is independent of recruitment density and the adult population reflects earlier recruitment success (Fig. 4.2; region A). Conversely, if the supply of recruits is sufficient to saturate the spatial resource, mortality of recruits becomes density-dependent as they grow.

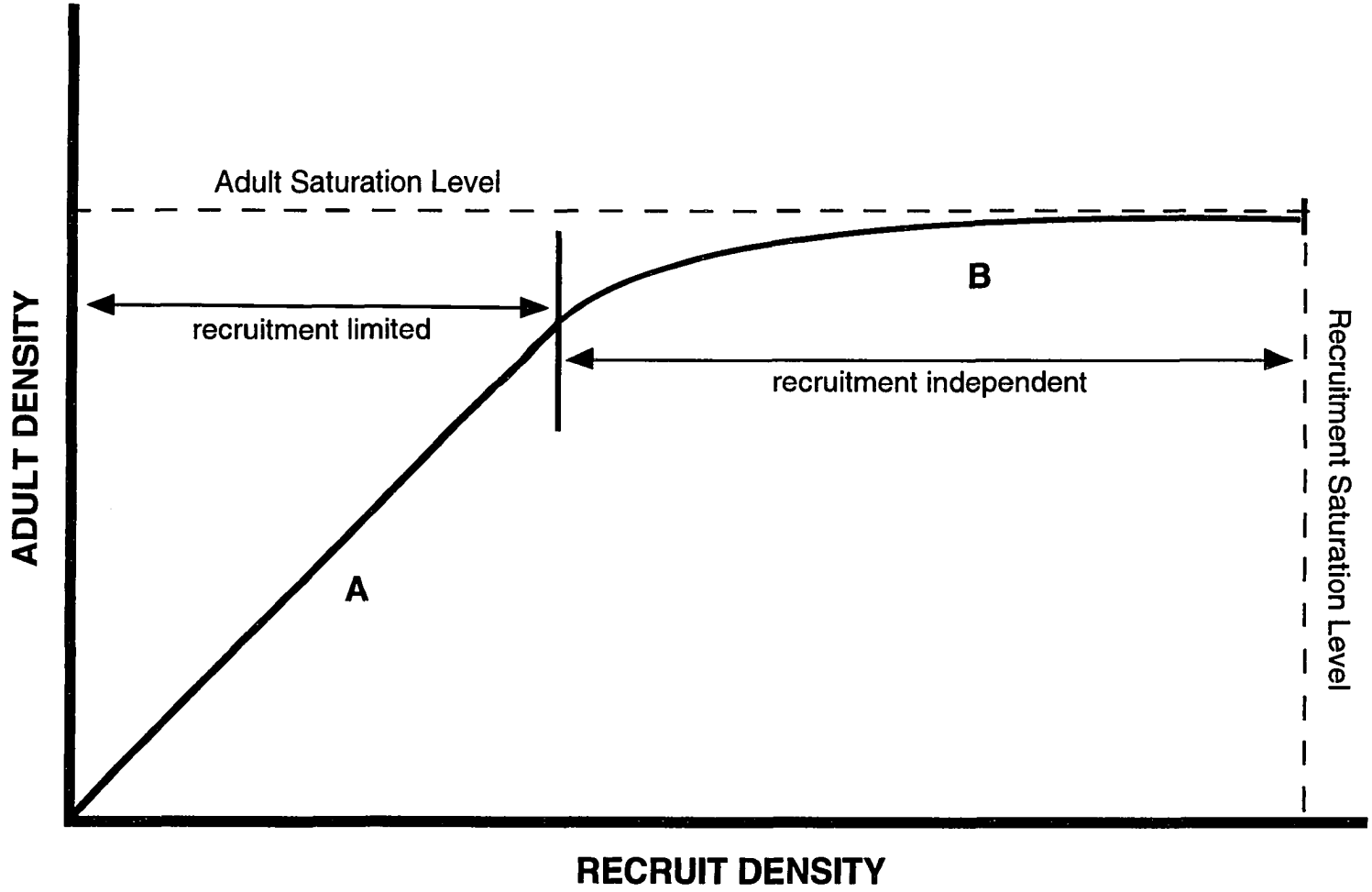


Figure 4.2: Idealized relationship between recruitment and adult density for a given benthic species.

Thus, if recruitment levels exceed adult saturation density, some individuals must be removed from the population, resulting in decoupling of recruitment and adult density (Fig. 4.2; region B). Under this scenario, population regulation will result from post-recruitment interactions (Karlson & Levitan, 1990; Holm, 1990; Hughes, 1990).

The consequences of variation in recruitment in marine systems and its role in regulating populations and influencing community structure has been the focus of much research in recent years. Experimental evidence from a variety of marine systems (such as tropical and temperate rocky intertidal habitats and coral reef systems) indicates that variable recruitment can regulate community structure (Doherty, 1983; Victor, 1983, 1986; Gaines, *et al.*, 1985; Doherty & Williams, 1988; Sutherland, 1987, 1990; Mapstone & Fowler, 1988; Roughgarden *et al.*, 1988; Menge & Farrell, 1989; Hughes, 1990; Karlson & Levitan, 1990; Raimondi, 1990; Menge, 1991; Doherty & Fowler, 1994). In these systems, the initial density of recruits defines the set of factors that subsequently affects adult density (Gaines & Roughgarden, 1985).

A central question regarding the importance of recruitment regulation to populations is how frequently does recruitment regulation occur and thus, how generalizable are the results from a particular study or system likely to be. Much of the research on recruitment processes and their population- and community-level importance has been conducted near the geographic center of species' ranges. In these locations, recruitment processes are likely to be less variable than at the fringes of species' geographic distribution where local reproductive failure and high mortality rates are more likely to occur, and

reliance on recruits from other source populations is more common (Bowman & Lewis, 1977; Lewis *et al.*, 1982; Karlson & Levitan, 1990).

In this study, the recruitment of intertidal barnacles was examined in southcentral Alaska. The sites under study, (59° 35'N, 151° 30'W) are near the northern limit of permanent barnacle populations on the Pacific coast. Northern geographic limits of barnacles in Alaska, as on the Atlantic coast (Barnes, 1957; Wethey, 1985), are likely determined by ice scour. North of 60° on the Bering Sea coast, intertidal barnacles are rare and ephemeral due to the physical effects of ice scour (O'Clair, 1981; O'Clair *et al.*, 1981).

The timing and magnitude of recruitment of intertidal barnacles was quantified and the factors causing variation in recruitment were identified. In addition, the relationship between recruitment density and population size of the resulting adult cohort was determined in order to test the hypothesis that recruitment success in this region is restricted, possibly by environmental extremes, and therefore the population is typically regulated primarily by recruitment processes rather than by post-recruitment interactions.

METHODS

Recruitment Patterns

The timing, magnitude, and scales of variation in barnacle recruitment and the role of recruitment in regulating barnacle populations was studied at Kasitsna Bay Point (KB) on the south shore of Kachemak Bay. Recruitment was quantified by counting settlers on both artificial plates and natural rock surfaces. Counts were made within an experimental design which allowed

the assessment of the influence of several factors on recruitment rate such as year, location, height on the shore, surface type, and predation (Fig. 4.3). Experiments were conducted at two locations, separated by approximately 200 m. At each site, recruitment was examined at two shore heights. The upper shore height, located in the upper third of the littoral zone (+3.5-4.0 m) was in the middle of the zone of maximum occurrence of *Semibalanus balanoides* and *Balanus glandula*. These two barnacle species occur together from Unalaska (Aleutian Islands) to the northern end of the Strait of Georgia, British Columbia (Pilsbry, 1916; Haven, 1973) and seem to be ecological equivalents in southcentral Alaska (O'Clair & Zimmerman, 1987). The lower height was located in the *S. cariosus* zone (+1.0-1.5 m MLLW). Within each shore height, 10 replicate arenas were placed in a randomized block design containing two treatments (five replicates of each treatment): (1) natural predation and (2) predators excluded. Each arena (= sampling unit) contained three samples: two artificial plates, and a natural rock surface (experimental design summarized in Fig. 4.3). Two artificial plates per sampling unit were used to determine recruitment variation on a small scale (centimeters). The rock surface in each sampling unit was used to provide a means to quantify barnacle recruitment artifacts resulting from use of an artificial surface.

Each artificial plate consisted of a 14 x 14 cm surface of 3.2 mm thick LEXAN plastic. Settling cyprids prefer irregular surface texture (Crisp & Barnes, 1954; Wethey, 1984b), so the plate surface was roughened with coarse (36 grade) sandpaper. A 6 x 9 cm study area was located in the center of the plate. The buffer zone around the study area was utilized to

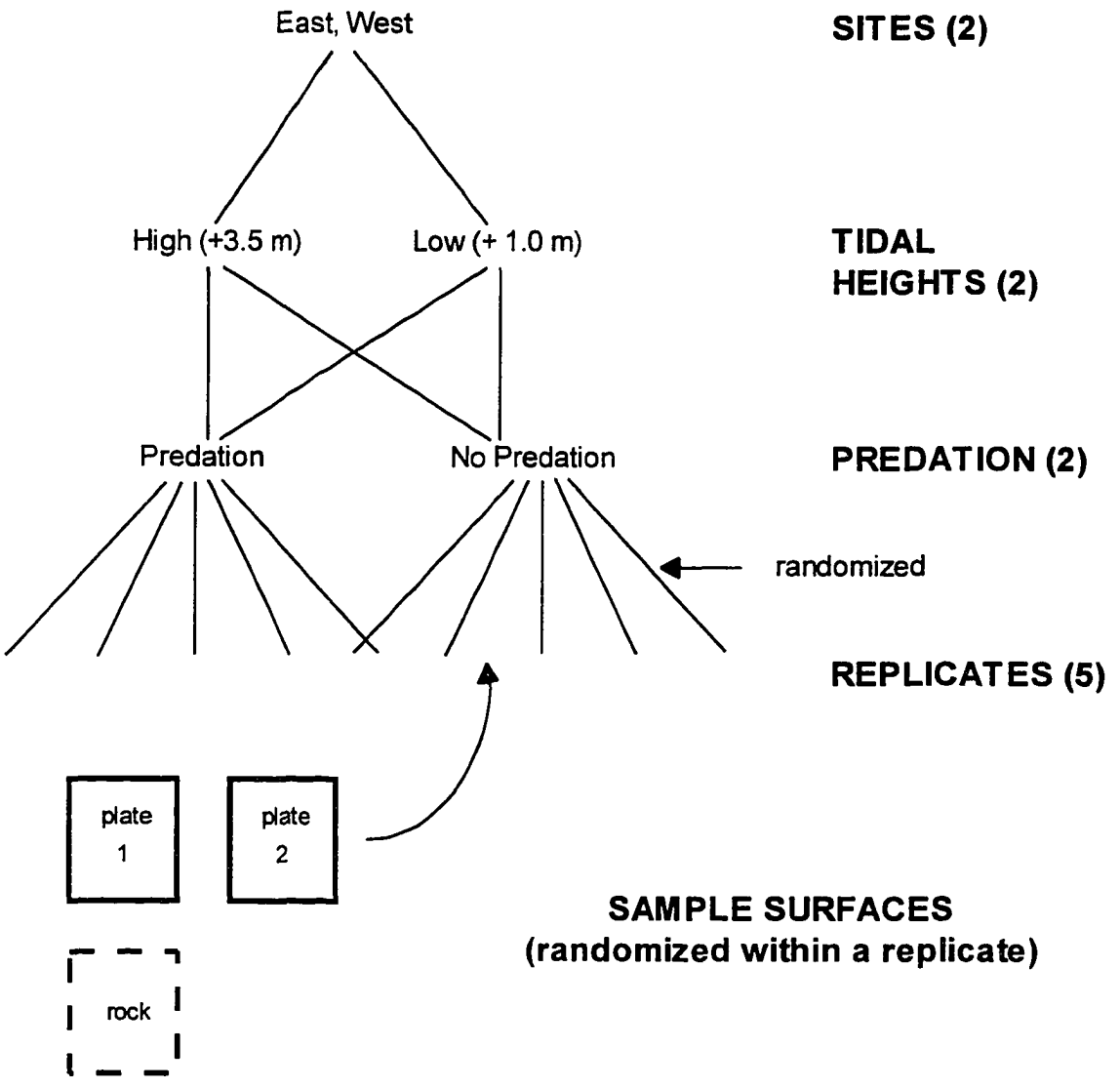


Figure 4.3: Schematic diagram of recruitment experimental design.

reduce artifacts due to edge effects. All plates were seasoned in seawater for at least 1 week prior to deployment. Both plates of a sampling unit were secured to a single backing plate (24 x 45 cm; 1 cm-thick high-density polyethylene) using plastic screws and wing nuts (Microplastics, Inc.; Flippin, Arkansas). This design allowed the plates to be easily removed seasonally for cleaning and replaced in their original locations. The backing plate was bolted to the bedrock with stainless steel screws and washers in plastic wall anchors imbedded in holes drilled into the rock using a gas-powered pneumatic drill.

Macro-predators were excluded with fences made of galvanized steel hardware cloth (0.635 cm mesh). The fences were secured between the backing plate and intertidal surface. Fences around rock surfaces were secured at the corners of the buffer zone. The fences extended 8-10 cm above the rock or plate surface. They were effective in excluding the principle predators in this region (*Nucella spp.*, *Leptasterias hexactis* and *Evasterias troschelii*). However, grazers such as *Littorina scutulata* and *L. stikana* and occasionally small limpets were able to crawl through or over the fences. They were removed with forceps during each census; particular attention was given to this task during the period of heaviest barnacle settlement to reduce bulldozing as a potential mortality source of barnacle recruits (Dayton, 1971). The nemertean, *Emplectonema gracile*, is a common predator of young barnacles in this region and is clearly small enough to move through the mesh fences. Nemerteans were noted at the recruitment sites, but were rarely detected feeding on barnacle recruits on the plates or rock test

surfaces only. As nemerteans forage during low tides, their activities would have been observable if an important source of mortality for recruits.

Plates were deployed and rock surfaces were mechanically cleaned of macro-organisms before early May, the beginning of barnacle settlement in the region. Once recruitment began, plates were censused every 5-7 days or as tides allowed. Censuses were conducted through the summer even after settlement had ceased, and at longer time intervals through autumn. A final census was taken in winter (December or January) when barnacle growth rates were minimal. Surfaces were censused by overlaying a 9x6 cm frame on the test area of the plate or rock. The frame rested against the wing nuts on plates or permanent screws on rock surfaces and allowed repeated censuses of the same area on subsequent sampling dates. When the density of recruits was high, the test areas were sub-sampled by dividing the frame into 10 equal regions and sampling four randomly chosen quadrats (coefficient of variation of sub-samples was 16.4%). Barnacle abundances were normalized to cm^{-2} for all analyses and presentation of results.

Abundance of Barnacle Larvae

Larval availability was estimated from weekly plankton tows from March to July 1992 and 1993. Two vertical tows were taken in the upper 10 m directly adjacent to the shoreline recruitment study sites (INSHORE) and at least 1 km off the tip of Nubble Point in the passage between Kasitsna Bay and Kachemak Bay (OFFSHORE). Samples were obtained with a 0.5 m diameter plankton net with 333 μm mesh and cod end. Larval abundances were determined from quantitative sub-samples of the contents of the tows. Sub-

samples were obtained by removing a known volume (typically 5-10%) with a Stemple pipette after the contents of the sample had been homogenized and counting all barnacle nauplii and cyprids in the sub-sample. The sub-sample volume was dependent on the density of larvae in the sample, with a target of 50-100 larval barnacles in the sub-sample. Abundances were normalized to m^3 for analysis.

Statistical Methods

Repeated measures analysis of variance techniques were used to elucidate differences in recruitment between years and to determine the factors causing variation in recruitment. After the significance of year on recruitment had been determined, Tukey's pairwise contrasts were used to reveal the manner of recruitment variation between years. Prior to analysis, all data were analyzed for normality and homogeneity of variances and were transformed when necessary. All analyses were conducted using PC SAS, version 6.04 (SAS, 1988).

RESULTS

Timing and Magnitude of Recruitment

The average date of the onset of barnacle settlement from 1991 to 1993 was May 10. Initiation of settlement varied by a maximum of 3 days during the 3 years, with settlement in 1991 and 1993 beginning on the same day. The consistency in the onset of barnacle settlement is remarkable considering likely year-to-year variation in physical factors such as water

temperature and current patterns, and of biological factors such as the spring phytoplankton bloom, which provides food for larval barnacles.

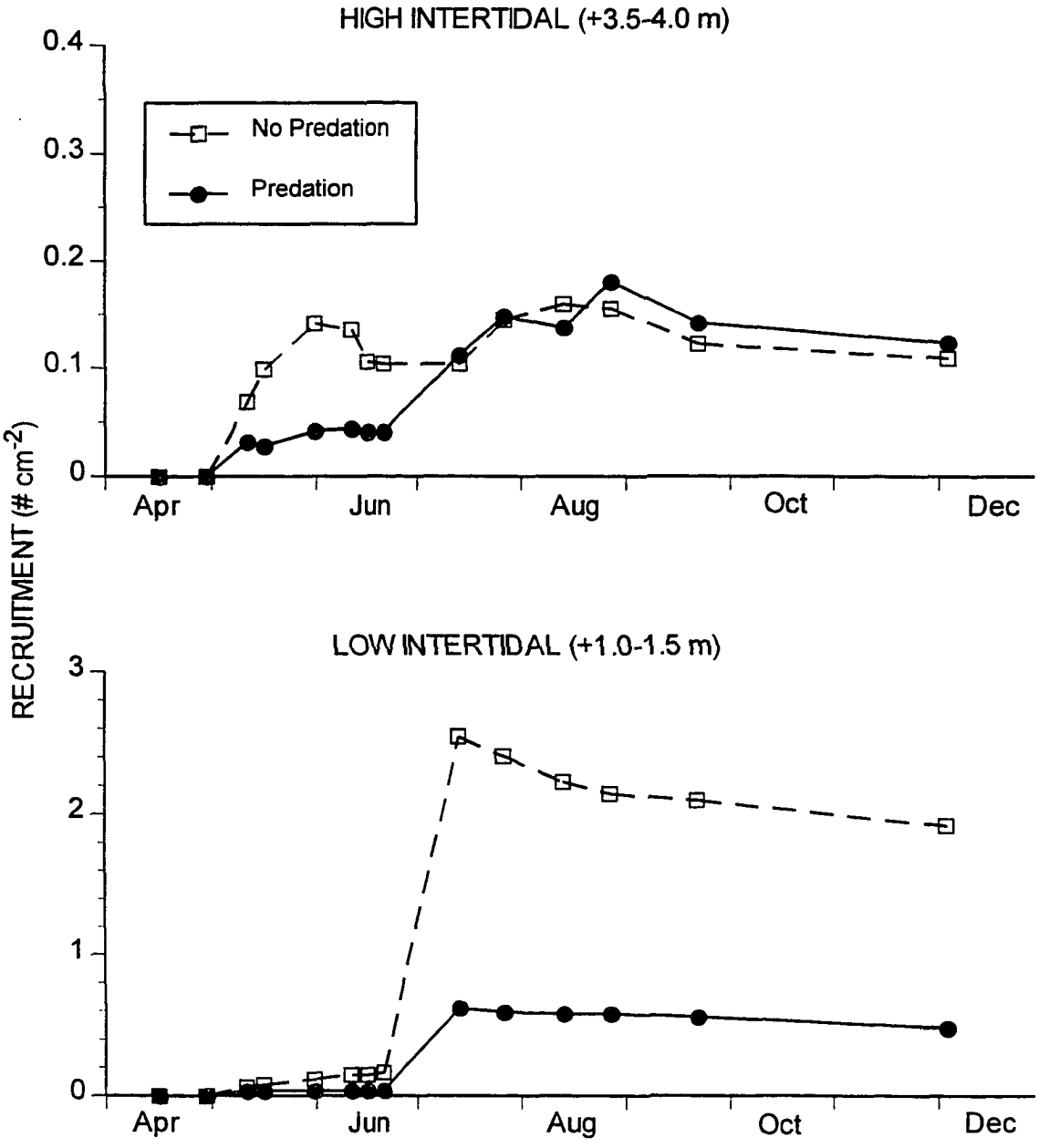
The similarity in the timing of the onset of barnacle settlement between years contrasts with a high year-to-year variation in the overall magnitude of recruitment and the temporal pattern of recruitment and mortality during the same years (Fig. 4.4a-c). in 1991, although recruitment began in early May, density of recruits on the shore did not reach a maximum until about mid-July when a settlement pulse occurred (Fig. 4.4a). Prior to that time, barnacle cyprids appeared sporadically in low densities. In 1992 and 1993, recruitment was initially heavy, resulting in a maximum density of recruits by the beginning of June, more than a month earlier than in 1991 (Fig. 4.4b,c).

The magnitude of recruitment also varied significantly between years (ANOVA: df=2; F=542.59; P<0.0001). Overall recruitment density in 1992 ($3.83 \pm 0.21_{SE}$ cm^{-2}) was 10 times greater than in 1991 (0.36 ± 0.28 cm^{-2}), and was also significantly greater than in 1993 (2.50 ± 0.19 cm^{-2}) (Table 4.1). Recruitment densities as high as 50 cm^{-2} were observed in 1992 while the maximum density in 1991 was only 8 cm^{-2}. Although overall recruitment was lower in 1993 compared to 1992, the highest single-sample recruitment density (71 cm^{-2}) occurred during 1993.

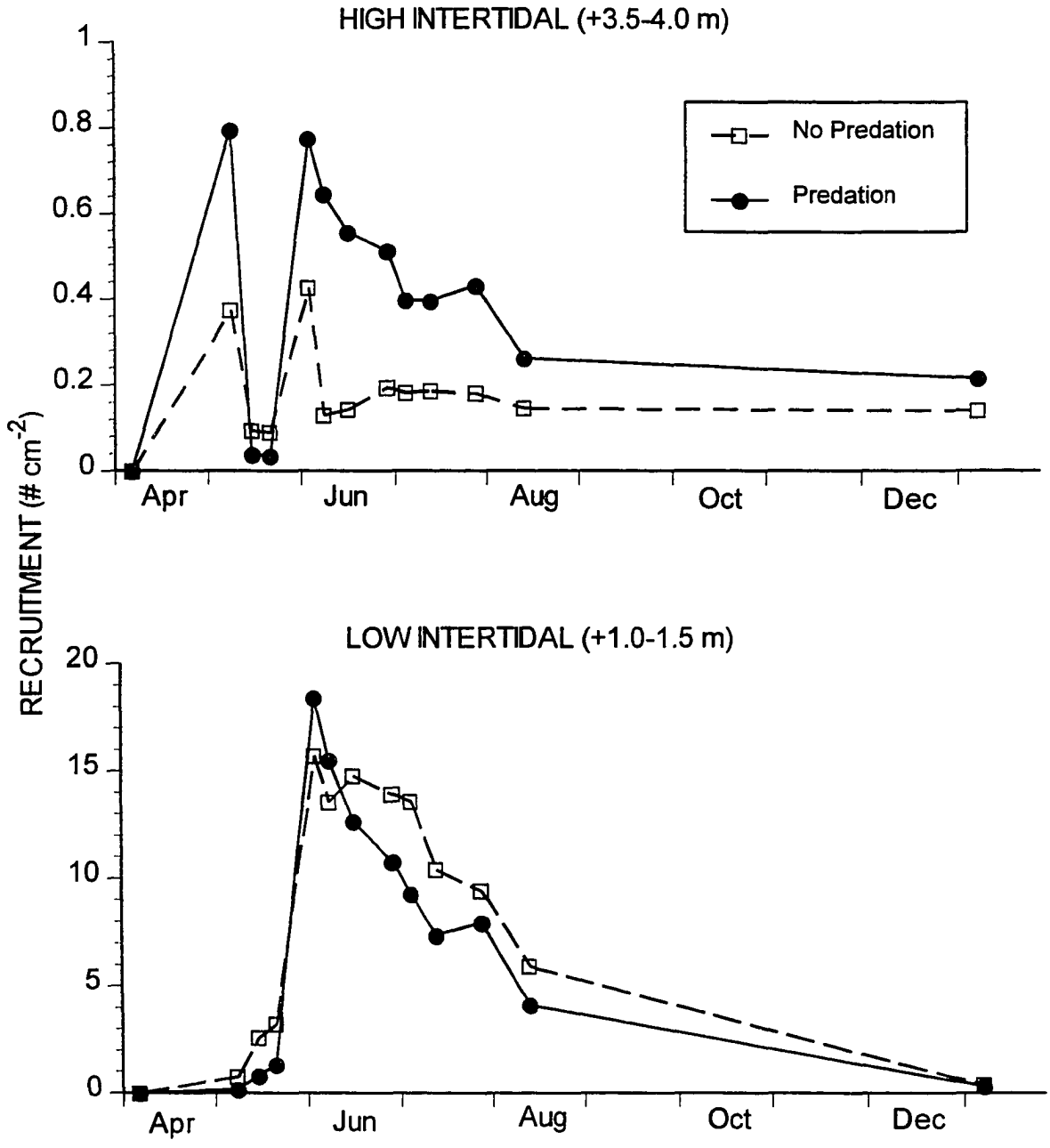
Recruitment densities in the upper intertidal were consistently below those in the lower intertidal, never exceeding 1 cm^{-2} in any of the 3 years. However, proportional survival of upper-intertidal recruits exceeded that of low intertidal recruits (Fig. 4.4), suggesting that biological factors play a greater role in recruit survival than physical stresses.

Figure 4.4: Mean barnacle recruit density (# cm^{-2}) on test surfaces (n=30) in 1991 (A), 1992 (B), and 1993 (C). Densities shown incorporate both the arrival of new settlers and mortality of existing recruits. Note different y-axis scales.

A. 1991



B. 1992



C. 1993

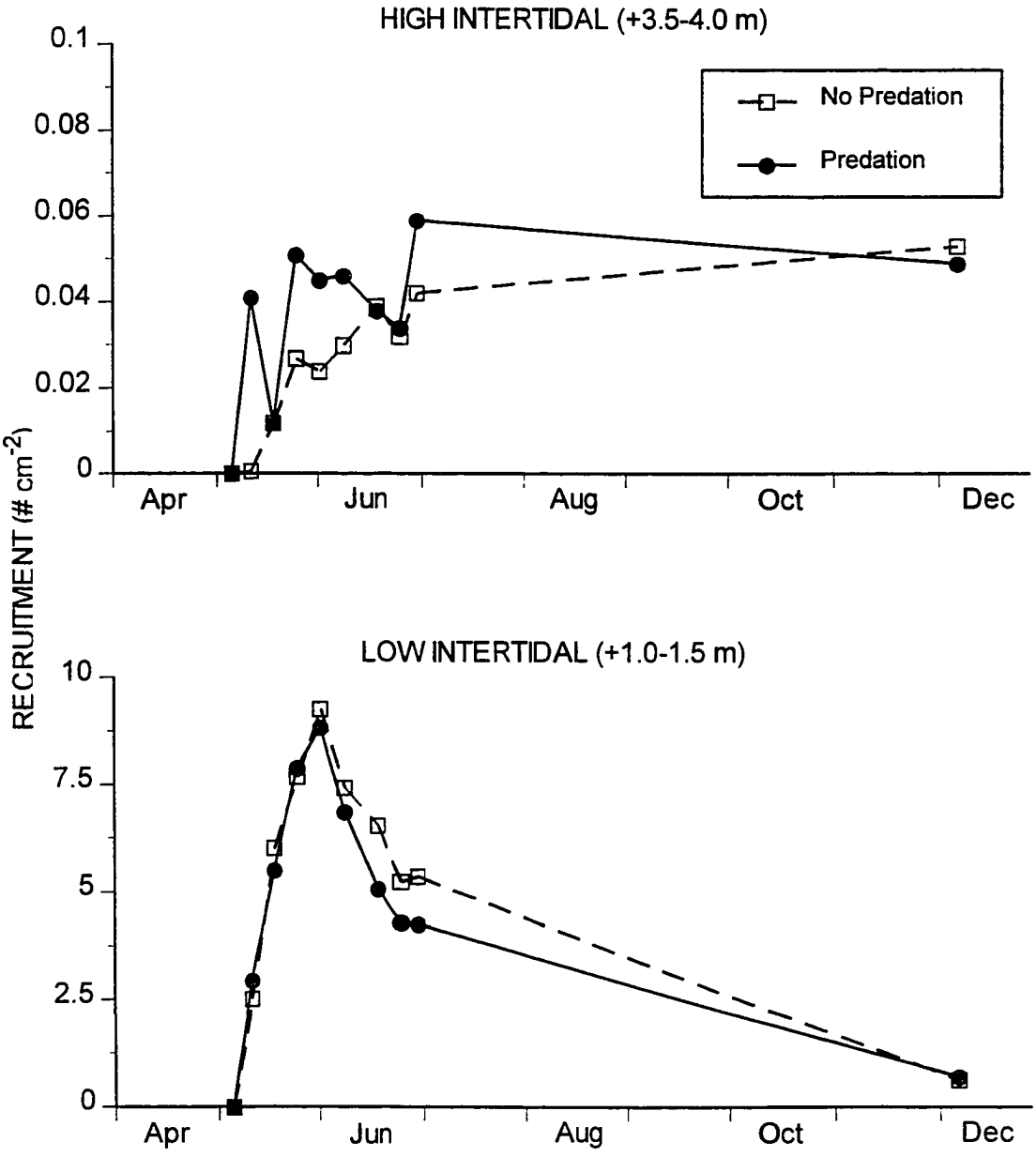


Table 4.1: Mean barnacle recruitment (# cm^{-2}±SE) in 1991, 1992, and 1993. Values are time-integrated over all sampling dates in a given year, except for Initial Density, which is the date of maximum recruit density. Significance groupings are for Initial Density and Total Recruitment and result from Tukey pairwise contrasts of means at an α=0.05 error level.

Factor	Level	Year		
		1991	1992	1993
Site	East	0.48 (0.05)	5.89 (0.35)	4.02 (0.33)
	West	0.23 (0.23)	1.78 (0.20)	0.90 (0.15)
Tide Level	High	0.09 (0.01)	0.28 (0.04)	0.03 (0.004)
	Low	0.63 (0.05)	7.45 (0.37)	4.87 (0.34)
Predation	No	0.55 (0.05)	4.05 (0.30)	2.56 (0.25)
	Yes	0.17 (0.15)	3.61 (0.29)	2.44 (0.28)
Surface	Artificial	0.43 (0.04)	3.84 (0.26)	1.18 (0.15)
	Natural	0.21 (0.02)	3.81 (0.33)	5.13 (0.46)
TOTAL (all variables pooled)		0.36 (0.28)	3.83 (0.21)	2.50 (0.19)
Initial Density		0.85 (0.16) Range: 0-8	8.71 (1.23) Range: 0-50	4.65 (0.88) Range: 0-71
Grouping		C	A	B

Factors Affecting Recruitment

As discussed above, the effect of year on recruitment rate was highly significant and likely to mask detection of significant effects of other factors on recruitment variation. Extreme differences in numbers of recruits between years can lead to differences in the influence of a particular factor between years. Thus, despite the slight loss of predictive value of a revised model, the year effect was removed from the model by analyzing each year separately. Thus, a 4-way analysis of variance was conducted separately for each year which examined the effect of site, intertidal level, predation and recruitment surface type on barnacle recruitment (Fig. 4.3). This approach provides a finer-scale resolution of the influence of specific factors within a year and allows assessment of how these factors vary in their influence among years.

Analysis of variance of square-root transformed data (Table 4.2) indicates that recruitment varied with both site and level in the intertidal during all 3 years of this study. The recruitment surface type (artificial plate vs. natural rock) had no effect except during 1993. Levels of predation caused significant variation in recruitment only during 1991. Although several sources of variation were included in the ANOVA, much of the variation in recruitment for all 3 years was due to factors other than those included in the model which accounted for 17%, 38%, and 53% of the variation in barnacle recruitment from 1991 to 1993 respectively.

Population Regulation

The data collected in this experiment were placed within the framework of the recruitment model (Fig. 4.2) to examine the relationship between

Table 4.2: Results of ANOVA examining factors influencing barnacle recruitment rate. Data are square root transformed.

	1991				1992				1993			
FACTOR	**DF**	**MS**	**F**	**P**	**DF**	**MS**	**F**	**P**	**DF**	**MS**	**F**	**P**
Site	1	5.69	25.36	0.0001	1	228.04	174.62	0.0001	1	183.11	189.86	0.0001
Level	1	22.64	100.92	0.0001	1	105.1	636.46	0.0001	1	486.95	505.28	0.0001
Surface	2	0.37	1.66	0.1902	2	2.83	1.71	0.1805	2	110.02	112.61	0.0001
Predation	1	9.18	40.90	0.0001	1	1.01	0.61	0.4349	1	1.00	1.05	0.3060
Error	1665	0.22			1524	1.65			1157	0.96		

recruitment and the adult barnacle population and thus to determine the importance of recruitment processes in regulating intertidal barnacle populations in Kachemak Bay.

The relationship between recruitment and adult population density is presented for 1991-1993 (Fig. 4.5). The date at which the highest density of recruits was observed was used as the initial density, and final density (= adult density) was the date of the last census of the season (December 1991, January 1993, and December 1993).

By the first winter following recruitment, the mean size of uncrowded individuals of the *B. glandula*/*S. balanoides* guild in 1993 (measured as the maximum basal diameter) was $8.69 \pm 0.36_{SE}$ mm (n=30), while the mean size of *S. cariosus* was $8.05 \pm 0.12_{SE}$mm (n=30). Furthermore, egg masses were detected in several individuals of this cohort. Feder & Keiser (1980) report that 70.5% of 1-year-old *S. balanoides* showed signs of reproductive development in Port Valdez, Alaska, and Newman & Abbott (1980) report that *B. glandula* settling in the spring are reproductive their first winter, suggesting that survivors in this study can be considered adults by their first winter.

The plots show the line of slope=1, representing a perfect linear relationship between recruit and adult densities and thus inferring recruitment regulation of the population. Although this analysis provides insight into the relationship between recruits and adults of a given year, it cannot assess the effect of accumulation of multiple year classes in the adult population. Recruitment and adult population density are highly correlated in 1991, a year when overall recruitment rate was relatively low. Initial recruitment explained 97% of the variation in adult density in this population. Variations in

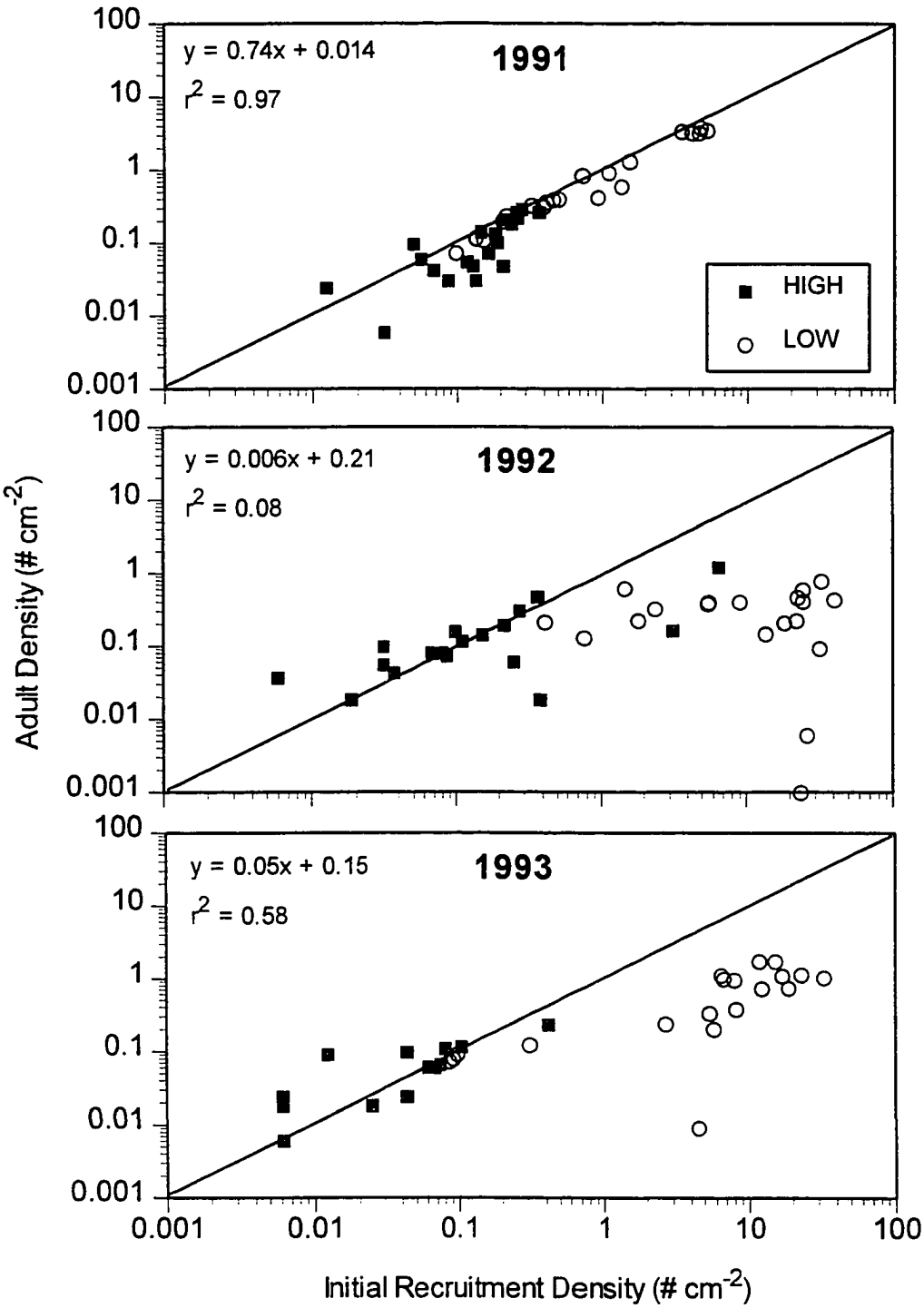


Figure 4.5: Relationship between initial recruitment and adult population density from 1991 to 1993. Solutions given include both tide levels combined in a year. The line shown represents a slope of 1.0, inferring a linear relationship between the two variables.

recruitment resulted in corresponding variations in adult density as most of the points fall close to the line. In 1991, therefore, the barnacle population was recruitment regulated because the characteristics of the recruitment cohort were carried through to the adult population.

The relationship between recruitment and adults was different in 1992 and 1993. Recruitment rates were much higher during those two years than during 1991 (Table 4.1) and recruitment test surfaces were often saturated with recruits. In 1992 and 1993 surfaces containing fewer recruits, primarily in the high intertidal, generally followed the same linear relationship as In 1991 (Fig. 4.5). At higher recruitment densities, the relationship between recruits and adults becomes decoupled. Consequently, recruitment and adult density varied independently at high recrultment rates during 1992 and 1993. Recruitment explained only 8% and 58% of the variation in adult populations in 1992 and 1993, respectively. The slope of the least squares line for these two years is 0.006 and 0.05. This is far different than the target slope of 1.0 which infers recruitment regulation of the population. In 1992 and 1993, post-recruitment, density-dependent processes were primarily responsible for determining adult population density, and recruitment regulation did not occur. Thus, the same population in the exact same location was regulated by different processes in successive years.

Abundance of Barnacle Larvae

The abundance of barnacle nauplii and cyprids in the nearshore coastal zone varied temporally both within the recruitment season and between years and spatially from inshore to offshore. Generally, larval abundance during

the recruitment season in 1992 and 1993 was greater inshore than offshore, but inshore-offshore abundances were linearly correlated (Fig. 4.6). In 1992, cyprid densities exceeded 700 m^{-3} in a single large inshore pulse at the beginning of June (Fig. 4.7a). At the same station, nauplii density never exceeded 300 m^{-3}, but exhibited 3 distinct pulses with densities >200 m^{-3}. Also in 1992, offshore cyprid density never exceeded 150 m^{-3} and maximum nauplii density was approximately 200 m^{-3}. Despite lower densities, the peak in larval density offshore was temporally similar to peak densities inshore. In 1993, nauplii had a peak inshore density of 1500 m^{-3} at the beginning of May (Fig. 4.7b). This high density was short-lived, as nauplii densities did not exceed 200 m^{-3} during any other time of the recruitment season. Cyprid densities failed to show a corresponding peak in abundance and never exceeded 150 m^{-3}. Offshore, nauplii were more abundant than cyprids during the entire sampling period but densities did not exceed 40 m^{-3}.

The results suggest that larval barnacle populations are open and therefore recruitment intensity is primarily controlled by transport processes and processes acting on larvae while in the plankton rather than by local reproduction. Although there is a relationship in larval abundance between inshore and offshore stations (Fig. 4.6) there was little similarity in the temporal pattern of nauplii and cyprids at a given station (Fig. 4.7). In closed populations, local reproductive output from adults is the primary source of local recruitment, and peaks in nauplii abundance should be followed by peaks in cyprid abundance. Here, the results indicate that cyprid density varied independently of nauplii density. During 1992, the peak in cyprid density was over twice as great as the previous peak in nauplii density. This

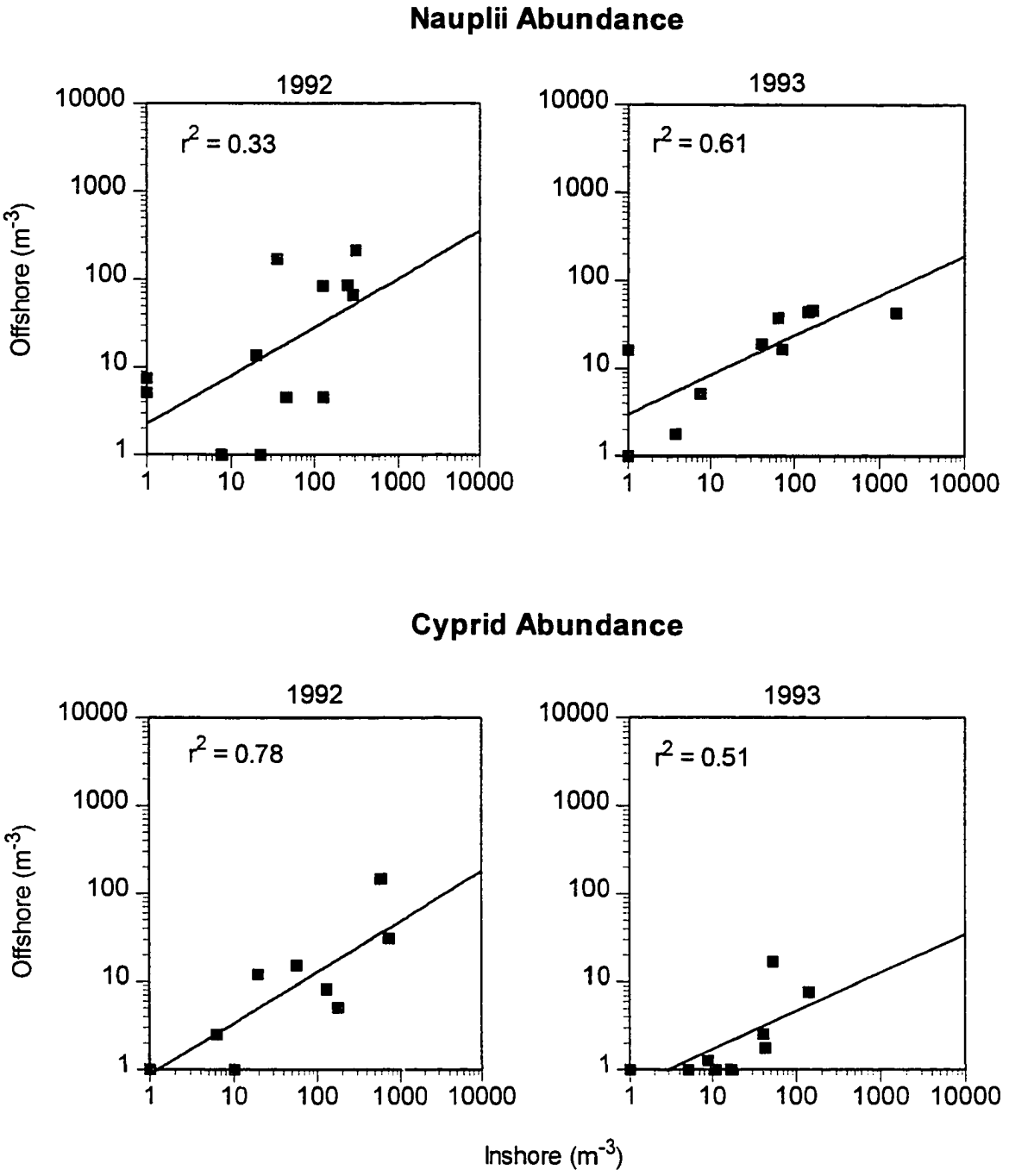
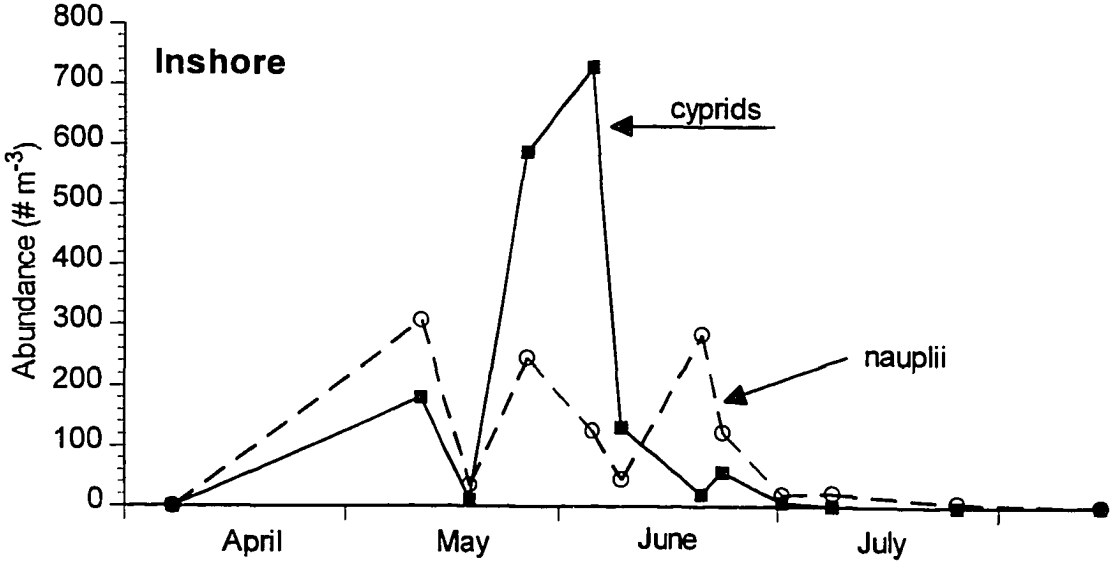
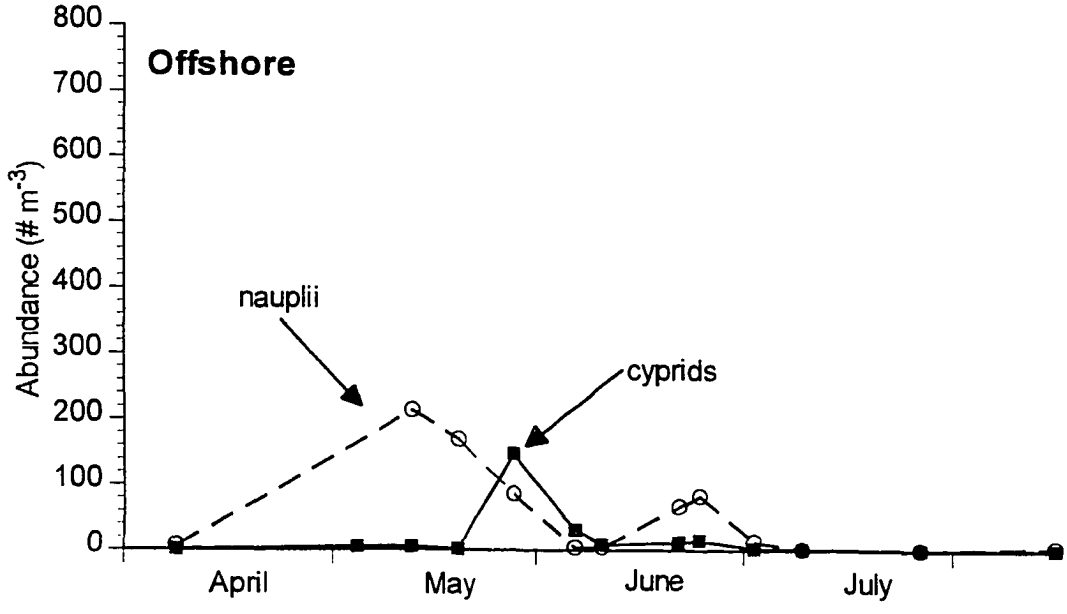


Figure 4.6: Relationship between inshore and offshore abundance of barnacle nauplii and cyprids in 1992 and 1993. r^2 values result from least squares regression.

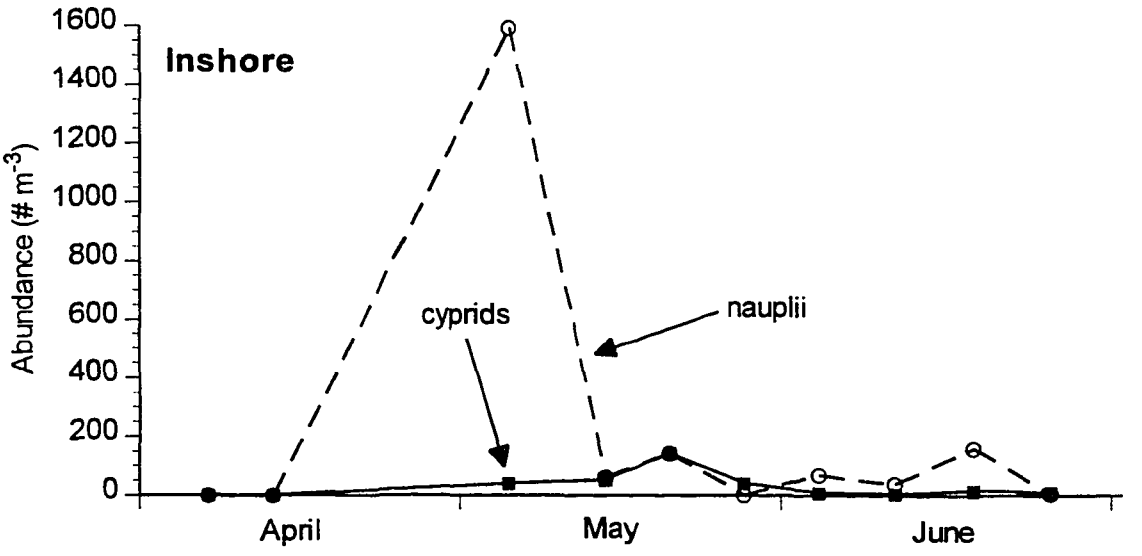
Figure 4.7: Temporal abundance of barnacle nauplii and cyprids at inshore and offshore plankton sampling stations in 1992 (A) and 1993 (B).

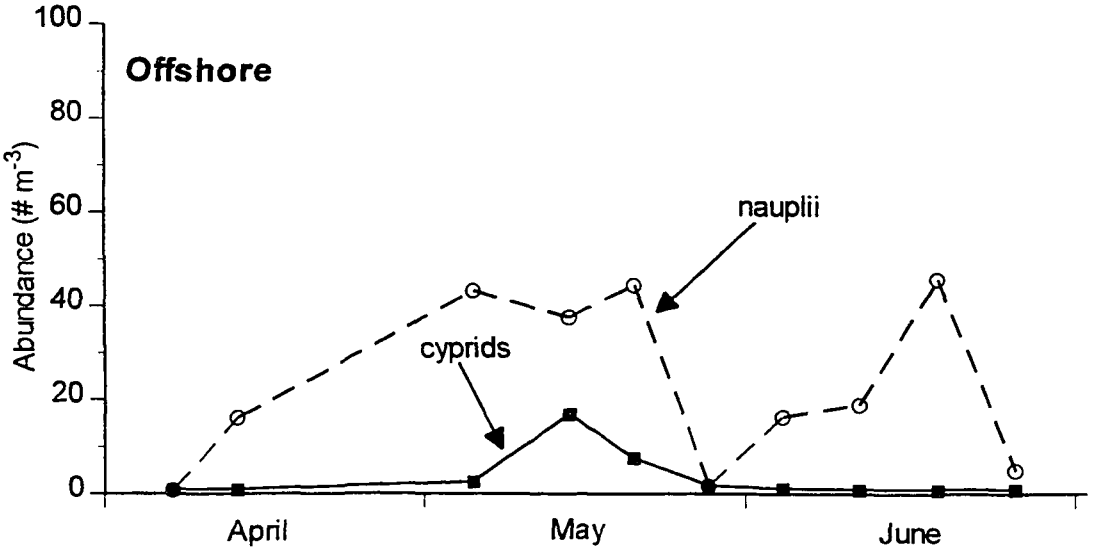
A. 1992





B. 1993





indicates that additional cyprids were transported from other areas, thus implicating physical transport processes as an important mechanism for providing potential recruits.

A positive relationship occurred between inshore cyprid density and recruitment (Fig. 4.8). Peaks in inshore cyprid density were followed in both 1992 and 1993 by pulses of recruitment. This underscores the importance of transport by oceanic currents to the nearshore area to local recruitment.

Discussion

In essence, all populations with pelagic larvae are ultimately recruitment driven because recruitment sets the "initial condition" (density of recruits) which determines the factors which will influence adult populations. If recruitment is variable and below adult saturation levels, then recruitment may also be limiting and thus regulate adult population dynamics.

Barnacle recruitment in Kachemak Bay varies in both time and space. Despite the predictable onset of initial settlement, the overall magnitude of recruitment was significantly different during each of the 3 years of this study, with recruitment in two consecutive years (1991 and 1992) varying by more than an order of magnitude. However, the ranking of recruitment sites in terms of recruitment density was consistent between years (East > West), a result similar to other studies (Caffey, 1985; Connell, 1985; Victor, 1986; Doherty, 1987; Raimondi, 1990; Sutherland, 1990; Fowler *et al.*, 1992). Recruitment also varied with tidal level (low > high). The consistently lower recruitment and mortality rates in the upper intertidal suggests that

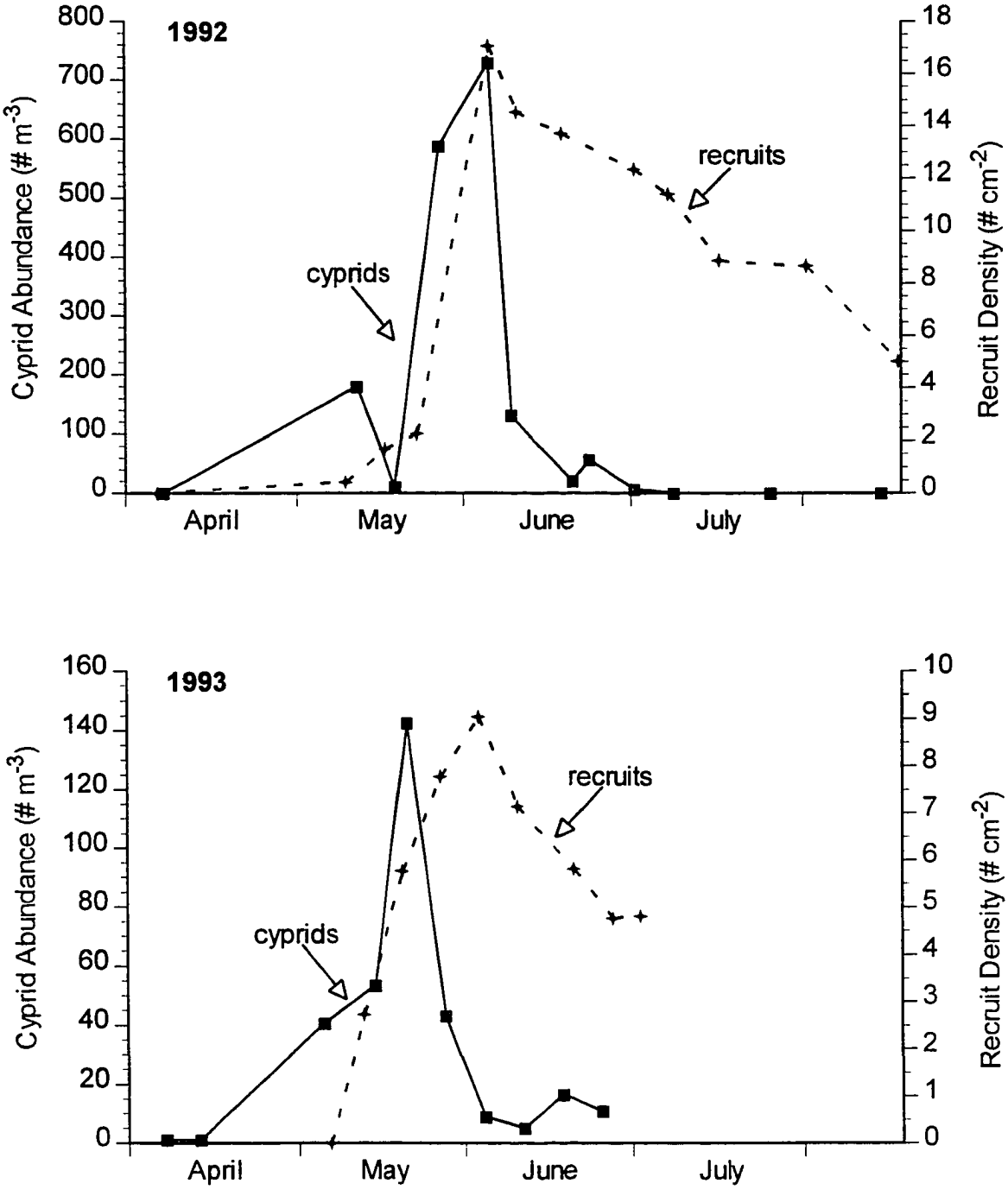


Figure 4.8: Relationship between inshore barnacle cyprid abundance and barnacle recruitment in the lower intertidal zone. Note differences in the y-axis scales.

populations in the upper intertidal are limited by recruitment more than lower intertidal populations.

High initial recruitment densities do not necessarily indicate high survival of recruits. For example, in 1991, maximum recruitment density in the lower intertidal was 1.6 cm^{-2} in both predation and predation-exclusion treatments combined, much lower than the maximum in 1992 (17.1 cm^{-2}) or 1993 (9.05 cm^{-2}) (Fig. 4.4). However, survival of recruits through early winter of the year of settlement was greater during 1991 (75%) than in 1992 (2%) or 1993 (7%). Thus, despite overall recruitment levels in 1991 below 1992 and 1993, the number of survivors in 1991 was actually the greatest of the 3 years studied. Hence, initial recruitment success does not guarantee the long-term success of a cohort in a population.

The effect of predation varied in importance between years. Predation significantly influenced barnacle recruitment only in 1991, a year when recruitment was much lower than either of the other two years. In 1992 and 1993, when overall recruitment was greater the effect of predation was negligible (Table 4.1; Table 4.2). Thus, the importance of predation is inversely related to the magnitude of barnacle recruitment. One explanation is that predators were swamped out by the extremely high density of recruits. The influence of predators in reducing the size of young barnacle populations can be overshadowed by density-dependent effects such as intraspecific competition for space. This would be important where densities of young, growing barnacles exceed the space available for adults.

As a result, barnacles may face a trade-off. Settling in high densities reduces an individual's chance of being preyed upon, as a recruit's probability

of being eaten varies inversely with the number of potential prey from which a predator has to choose (i.e. safety in numbers). Conversely, settling with a large number of conspecifics creates intense competition for space where only a few of the settlers can possibly survive to adulthood. In 1993 for example, there were areas where recruit density was >70 cm^{-2}. If the maximum density of adults is 2-3 cm^{-2} (from Fig. 4.5), then only 4% of the initial recruits could survive to adulthood at such high recruitment densities. Other factors such as predation and physical factors (waves, desiccation, etc.) reduce survival even further; the average survival in 1992 was 2%. Because barnacles have direct fertilization, being located in a dense population assures a mating opportunity and provides more potential mates for an adult, thus increasing potential fitness. Evolutionarily, there must be a trade-off between settling in high densities that reduce predation and increase potential matings and settling in low densities that reduce competition for space. As settlement density is not uniform, there is likely an averaging effect from the standpoint of the fitness of the adults that produced the recruits.

Although predation can be an important factor affecting populations of young growing barnacles, its effect is not predictable. The importance of predation seems to be determined by the density of initial recruits. Recruitment sets the initial condition for post-recruitment interactions and determines which post-recruitment factors are important (Caffey, 1985; Gaines & Roughgarden, 1985; Fairweather, 1988; O'Neill, 1989).

Recruitment was only limiting during 1 of the 3 years of this study, thus recruitment regulation was not occur predictable in this population. When

recruitment was sparse (in 1991), the adult population reflected the numerical characteristics of the recruitment cohort indicating recruitment regulation of the population during that year(Fig. 4.5). In contrast, recruitment was high 1992 and 1993, generally exceeding the adult saturation level and resulting in extensive density-dependent mortality as recruits grew. Adult density was tightly coupled to recruitment in those quadrats exhibiting low recruitment. The relationship between recruitment and the size of the adult population was dependent upon the density of initial recruitment (Connell, 1985).

Recruitment levels exceeded adult saturation density during 2 of 3 years of this study, indicating that recruitment is probably not limiting in this population. These results only partially support the contention that populations near the edges of their geographic distributional limits are more likely to be limited by recruitment (Bowman & Lewis, 1977; Lewis *et al.*, 1982; Karlson & Levitan, 1990). Recruitment failure, is thought to be more frequent in edge zones because of sub-optimal conditions imposed by increased environmental stress. In this study, where greater environmental extremes occur than at lower latitudes on the west coast, recruitment was only limiting in one out of three years and overall was ample to maintain local populations.

Nearshore oceanic processes are a necessary element in providing potential settlers to the shoreline. One of the principle features of supply-side ecology is the decoupling between local reproductive output and local recruitment. These open populations must rely on transport processes and larval behavior to provide adequate larvae for settlement. A link between recruitment and oceanographic transport has been widely suggested and demonstrated in some systems (Kendall *et al.*, 1982; Cameron & Rumrill,

1982; Gaines *et al.*, 1985; Roughgarden *et al.*, 1986; Shanks, 1986; Victor, 1986; Ebert & Russell, 1988; Reed *et al.*, 1988; Roughgarden *et al.*, 1988; Black & Moran, 1991; Farrell *et al.*, 1991; Gaines & Bertness, 1992, 1993). The temporal relationship between cyprid abundance and recruitment intensity in this study also suggests that oceanic transport processes are a critical element in local patterns of recruitment in Kachemak Bay (however, see cautions in Gaines & Bertness, 1993). Pulses of recruitment followed peaks in nearshore cyprid abundances which were extremely variable in time. These patterns suggest that successful recruitment occurs when transport moves water laden with larvae close to the shoreline (Caffey, 1985).

In summary, recruitment of intertidal barnacle populations in Kachemak Bay Alaska is characterized by a suite of both stochastic and deterministic processes. Predictable events included the spatial pattern of recruitment variation (site-to-site and tidal level) and the timing of recruitment during the year. Stochastic variation occurred in the overall magnitude of recruitment between years and the importance of pre- or post-recruitment factors in regulating the local population. Thus, recruitment in this system reflects the interactive influence of deterministic and stochastic sources of variation (Doherty & Williams, 1988; Fowler *et al.*, 1992). The results of this study provide partial support for the conclusions of early workers which focused on the importance of post-recruitment interactions to population dynamics and community structure of west coast rocky intertidal communities. The hypothesis of increased incidence of recruitment failure resulting from greater environmental extremes at the fringes of a species' geographic distribution was not entirely supported.

SUMMARY

Time-integrated yearly recruitment levels ranged from 0.36 to 3.83 cm^{-2} from 1991-1993. Average initial recruitment densities ranged from 0.85 to 8.71 cm^{-2}, with recruitment densities at individual test sites exceeding 70 cm^{-2}. Site-to-site variation in recruitment was significant but the ranking of sites was consistent between years, as was the variation in recruitment with height on the shore (low > high). Predation significantly affected the cohort of recruits only during one year (1991), a year of comparatively low recruitment. 1991 was also the only year during which there was a linear relationship between initial recruitment and adult density of the resulting population across all recruitment densities. In 1992 and 1993, years when overall recruitment densities were much higher, density-dependent mortality was evident and resulted in decoupling of recruitment and adult density. At this location near their geographic limit, recruitment densities of barnacles exceeding the adult saturation point were common in the lower intertidal. Consequently, regulation of this population was principally via post-recruitment, density-dependent interactions (i.e. intra-specific competition) rather than by recruitment even though recruitment may be the major structuring factor in the upper-intertidal or years in which recruitment density is below levels leading to adult saturation.

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CHAPTER 5

PREDATOR CONTROL OF PREY POPULATIONS MEDIATED BY CATASTROPHIC DISTURBANCE: *NUCELLA-MYTILUS* INTERACTIONS

INTRODUCTION

The ability of an organism to respond to variation in its environment is of paramount importance to its success in a local community. Interactions between species in a community occur within a framework set by species' tolerances of the physical parameters characteristic of a particular habitat.

Superimposed upon characteristic and predictable patterns of environmental variability are disturbance events (Sousa, 1979, 1984; Dethier, 1984). Disturbance has been characterized as "a discrete, punctuated killing, displacement, or damaging of one or more individuals (or colonies) that directly or indirectly creates an opportunity for new individuals (or colonies) to become established" (Sousa, 1984 p. 356). Both physical and biological processes may act as agents of disturbance (Sousa, 1984), and disturbance events may vary in frequency, severity, and predictability (Dethier, 1984; Sousa, 1984). At one end of a disturbance continuum are chronic, low-intensity, and relatively predictable events to which species may be able to adjust (e.g. exposure to wave action). At the other end of the continuum are catastrophic events which are acute, rare, and unpredictable, which affect many species, cause extensive mortality, and at least temporarily, alter community structure (Harper, 1977; Dethier, 1984).

Stochastic disturbances, because of their unpredictable nature and depending upon their severity, frequency, and extent of effect on individual species within a community, may be an important factor in structuring communities. These disturbances may influence the community not only in their immediate and direct effects, but also through alteration of interactions between component species in a community. Additionally, effects of

disturbances may be exacerbated in species which are living in habitats at or near their limits of physiological tolerance (Bowman & Lewis, 1977; Lewis *et al.*, 1982; Sousa, 1984).

Thus, the distribution and abundance patterns of an organism results from the dynamic interplay between environmental and biological forcing functions, and may vary in response to the interaction between these influences or in response to stochastic disturbance events. Rocky intertidal habitats are particularly amenable to examining the influences of physical forcing functions on species distributions and interactions because physical gradients are compressed and very often are well defined, and also because many rocky intertidal species typically are sessile or have very limited motility and thus are easy to observe and manipulate.

Mussels are a common constituent of rocky intertidal communities throughout the world (Soot-Ryen, 1955; Seed, 1976; Suchanek, 1986), and the Pacific coast of North America is no exception (Ricketts *et al.*, 1985). The ubiquity in the geographic distribution of mytilids is due, at least in part, to their tendency to exhibit r-strategist characteristics (Pianka, 1970). Mussels settle densely and grow quickly to reproductive size (under ideal conditions, *Mytilus edulis* (L.) may grow to a size of 60-70mm within 12-18 months) (Seed, 1969a, b, 1976, and references therein), often occupying up to 75-80% of the substratum soon after arrival at a location of unoccupied space (Suchanek, 1978). These characteristics, combined with relatively high mobility compared to other space-occupying intertidal species, lead to mussels' competitive superiority (Seed, 1976; Menge, 1976; Lubchenco & Menge, 1978), and often resulting in exclusion of other species in broad,

extensive mussel bands in the mid-intertidal; a distinctive feature common to many rocky shorelines (Stephenson & Stephenson, 1972; Ricketts *et al.*, 1985; Suchanek, 1986).

At temperate latitudes on the western shoreline of North America, space in the lower intertidal is often dominated by *Mytilus californianus* Conrad, especially on exposed shores (Paine 1966, 1974, 1980). The smaller, competitively subordinate *M. trossulus* (see Koehn, 1991; McDonald *et al.*, 1991; Morgensen *et al.*, 1991 for current nomenclature) occupies disturbance-created refuges in *M. californianus* beds, zones above *M. californianus*, and habitats less exposed to wave action (Suchanek, 1978, 1981). In Alaska, however, *M. trossulus* typically dominates much of the littoral zone (covering as much as 5.5 vertical meters of space in Glacier Bay; Suchanek, 1986). *M. californianus* is rare in Alaska (Ricketts *et al.*, 1985) and its distribution is restricted to tidepools, extremely low intertidal zones, and sublittoral habitats. The restricted distribution of *M. californianus* in Alaska results from its susceptibility to freeze-related mortality (Suchanek, 1978, 1986). The success of *M. trossulus* in occupying and often dominating rocky intertidal space over large geographical areas is due, in part, to its high tolerance of a wide range of environmental conditions including temperature (Seed, 1969b).

Mussels are preyed upon by a variety species including predatory snails, sea stars, crabs, fish, sea otters, sea birds and shore birds (Suchanek, 1986), and even terrestrial vertebrates such as mink (personal observation). As a result, predation has been shown to set the lower intertidal limit of mussel survival in many intertidal habitats throughout the world and with many

different predators or suites of predators (Suchanek, 1986). However, mussels usually persist higher on the shoreline in a refuge zone above the level of high predator abundance. As a result, predator control of mussel populations throughout their entire vertical range is rare.

In Kachemak Bay, southcentral Alaska (Fig. 2.1), the principal predator on *M. trossulus* is the predatory gastropod *Nucella lima* (Kincaid, 1964). *N. lima* occupies a broad vertical range in the mid-intertidal zone which overlaps that of *M. trossulus*. Other benthic predators occur in either low densities or are found in low intertidal zones not overlapping with mussels, so that their effect on mussel populations is negligible (personal observation).

In January, 1989, an extended (>3 week) severe freeze (recorded temperatures as low as -31°C) coincided with a spring low tide series in southcentral Alaska (Fig. 3.1). The freeze substantially altered the structure of rocky intertidal communities by causing extensive mortality of some constituent species (see Chapter 3). *M. trossulus* was one of the species severely affected and suffered extensive mortality in the upper part of its vertical range. *N. lima* did not seem as severely affected because it winters at lower levels in the intertidal (personal observation). Since the freeze, patterns of mussel recovery have been atypical compared to expectations based on the recruitment and growth characteristics that mussels typically possess. Although rates of recovery from disturbance in mussel beds vary, the process is thought to be deterministic (Suchanek, 1986) with mussels soon returning to dominance in the mid-intertidal zone. However, in Kachemak Bay, more than three years after large numbers of mussels were

removed from the community, the "mussel band" on shorelines was rare and patchy.

This disturbance provided a unique opportunity to observe the influence of a stochastic disturbance event and to determine its effect on community structure in terms of its initial impact and through the long-term alteration of predator-prey interactions between resident species. This paper documents the patterns of *M. trossulus* distribution and abundance relative to recovery from a catastrophic disturbance event. The hypothesis tested was that high predation rates by ***N. lima*** were responsible for the delayed recovery of *M. trossulus* and its failure to regain spatial dominance in many locations.

METHODS

Density, Cover, and Size Determinations

Nucella and *Mytilus* abundances were determined during the summer of 1992. Initially, *Nucella* density was estimated in Kasitsna Bay, a small pocket embayment on the south shore of Kachemak Bay, at two sites separated by approximately 200 m. *Nucella* densities were determined from 10-30 randomly located 0.25 m^2 quadrats which were cast blindly in the vertical zone of ***Nucella's*** greatest occurrence (+1.5 to +3.5 m). The number of randomly located quadrats per census varied with time, however the number of quadrats was consistent between sites during a given census. All snails in quadrats were counted and measured to the nearest 1 mm. Snail size was measured as the length from the apex to the end of the siphonal canal (total

length along the axis of coiling). Censusing was conducted in four consecutive months beginning in April 1992 and again in December 1993.

In July 1992, *Nucella* density was determined, using the procedure described above, at both Kasitsna Bay and Nubble Point (Fig. 2.1). Nubble Point is an exposed rocky outcropping approximately 2 km from the Kasitsna Bay sites and is isolated from neighboring rocky intertidal habitats by several hundred meters of sand and gravel beaches. In the same (n=30) quadrats that were censused for *Nucella* density, percent cover of *Mytilus* was estimated using the point frame method. A 0.25 m^2 frame with a grid of 81 evenly spaced points (every 5 cm on each axis) was placed over the quadrat and aligned with the quadrat corners. Cover (%) was determined as the number of points directly over mussels compared to the total number of points in the grid. Long-term temporal trends in mussel cover were obtained from photographic censuses of permanent quadrats at each of these sites (described in detail in Chapter 3).

Causes of *Mytilus* Mortality

To estimate the proportion of mussel mortality directly attributable to *Nucella* predation versus other sources of mortality, the valves of dead mussel shells were examined at Kasitsna Bay and Nubble Point. *Nucella* attack mussels by drilling through one of the valves of the shell. Drilling is done with alternating applications of enzymes by the accessory boring organ and the radula to scrape away weakened calcium carbonate (Carriker & van Zandt, 1972). This process leaves a characteristic drill hole in the shell,

hence mortality resulting from *Nucella* predation is easily distinguishable from other mortality sources.

The first 100 empty *Mytilus* shells encountered in each of two size classes (<25 mm, >25 mm) at Kasitsna Bay and Nubble Point were inspected for drill holes caused by *Nucella* predation. Only remains with both valves attached were used in the census.

Effect of *Nucella* Predation on *Mytilus*

The potential role of *Nucella* in regulating mussel populations in the field was determined by experimentally manipulating the density of snails in mussel beds. Cages were used to maintain constant snail densities at test sites in mussel beds.

Small cages (20 x 20 x 10 cm), made of 0.635 cm mesh galvanized steel hardware cloth, were established in mussel beds at Kasitsna Bay where initial mussel cover exceeded 90%. Average sizes of mussels in beds where cages were placed ($27.9 \pm 1.52_{SE}$ mm; n=40) were consistent (ANOVA: df=1,78 F=1.49, P=0.23) with the size of mussels outside cages ($25.6 \pm 1.13_{SE}$ mm; n=40). Each cage was randomly assigned one of three *Nucella* density (= level of predation) treatments: normal density (5 snails), high density (10 snails), and a control which contained no snails. *Nucella* densities used were based on the average *Nucella* density (131.6 m^{-2}) during the most recent census. There were eight replicates per treatment. The mean size of the snails ($17.65 \pm 0.25_{SE}$ mm; n=120) used in the cages was smaller (ANOVA: df=1,452 F=9.69, P=0.0020) than the size of the snails in the most recent census ($19.26 \pm 0.49_{SE}$ mm; n=334).

Mussel cover in the cages was estimated by overlaying a grid of 100 points located on a clear acetate sheet atop the mussel bed within each cage and determining the proportion of total points which were directly over mussels. Each cage was censused at the initiation of the experiment and every two weeks during the eight-week duration of the experiment.

RESULTS

Trends in *Mytilus* and *Nucella* Cover

In April 1989, only a few months following the freeze, live mussels were rare in the mid-intertidal. In this zone, extensive stands of gaping mussels, still attached to the rocks, were noted (personal observation), and often, not a single live individual was found in these dense mussel beds. Additionally, conspicuous windrows containing thousands of mussel shells were commonly observed on beaches. By the summer of 1989, most of the dead mussel shells previously attached to rocks had fallen off or been washed away by wave action. Live mussels initially occupied essentially no space in a zone where they are normally abundant. (Fig. 3.5), underscoring the severity of the freeze to mussel populations.

Mussels exhibited some recruitment during the summer following the freeze (Fig. 3.5), but their cover did not increase rapidly through high recruitment and growth rates as would be expected from the literature (e.g. Seed, 1976; Suchanek, 1978). On the contrary, following recruitment mussel cover decreased for the remainder of 1990 and into the spring of 1991. This pattern of moderate recruitment followed by a decrease in cover is repeated

in 1991 and 1992. Consequently, 3.5 years after the freeze, mussel cover did not increase appreciably beyond low levels and could not be considered a spatial dominant.

Nucella density varied markedly between summer and winter. In winter months, *Nucella* was scarce in the mid-intertidal (December 1993: $0.80 \pm 0.37_{SE} m^{-2}$; n=20). The few snails that were found higher in the intertidal were usually restricted to moist crevices and small tide pools (personal observation), however feeding apparently does not completely cease during winter, as one (of a total of only 4) of the snails in the winter census was observed feeding on a mussel.

In April, *Nucella* density at Kasitsna Bay was relatively low, indicating a transition between winter and summer densities and by May, densities increased about three-fold (Fig. 5.1). The summer increase in snail density is coincident with peak barnacle recruitment, a major food source for small snails. Hatchling snails readily consume metamorphosed barnacle recruits (Gosselin & Chia, 1993; personal observation)

Although *Nucella* densities differ at the two sites in Kasitsna Bay by 35%, summer densities (April data excluded) within a site remained relatively constant (ANOVA, Site 1: df=2,27 F=1.14, P=0.34; Site 2: df=2,27 F=1.21, P=0.31). At both sites, *Nucella* density in April was significantly less than during the summer months (ANOVA, Site 1: df=1,48 F=81.89, P<0.0001; Site 2: df=1,48 F=146.83, P<0.0001). *Nucella* size distributions at both sites exhibit a bimodal distribution (Fig. 5.2). The shift in the first peak to larger sizes during the summer season reflects growth in the previous year's cohort. The larger size peak may encompass several cohorts. In a preliminary

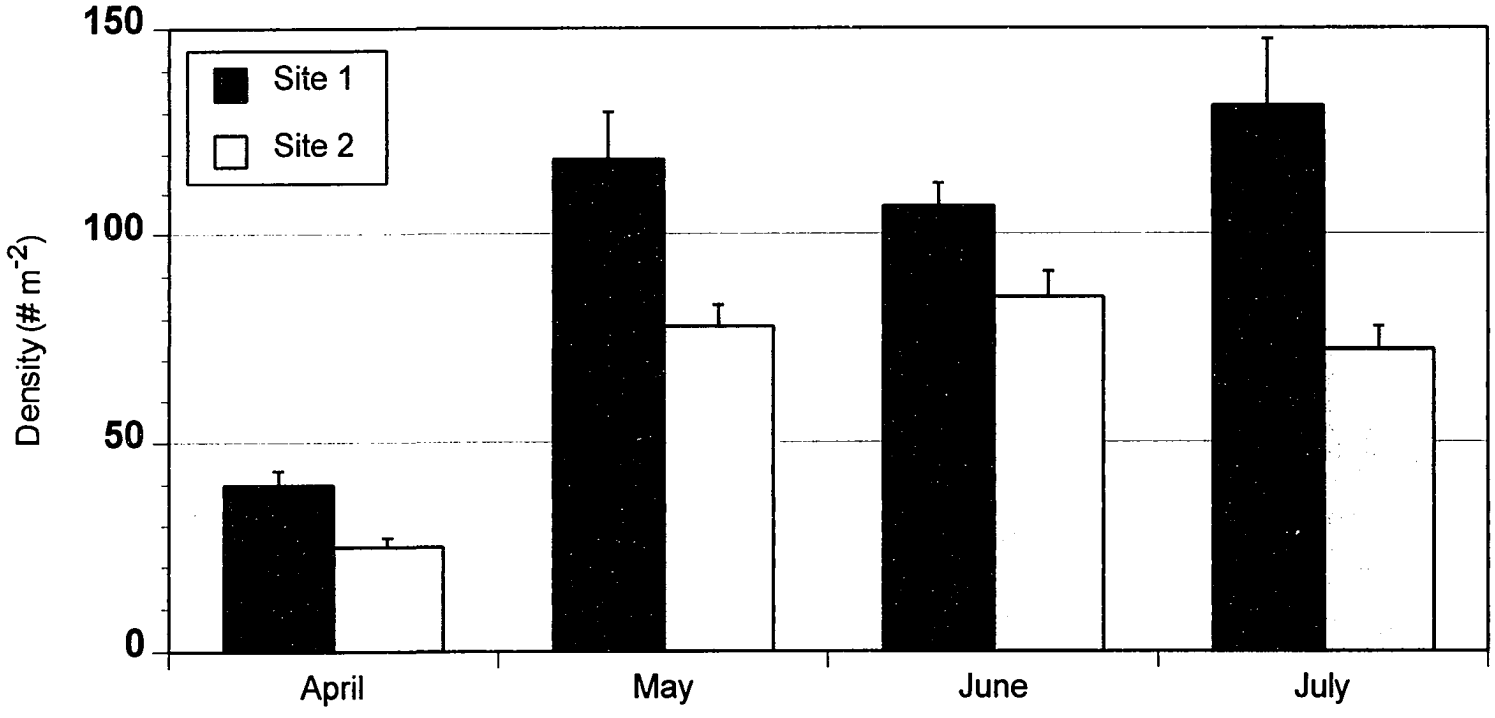

Figure 5.1: Variation in *Nucella lima* density (+SE) at two locations in Kasitsna Bay during the spring and summer of 1992.

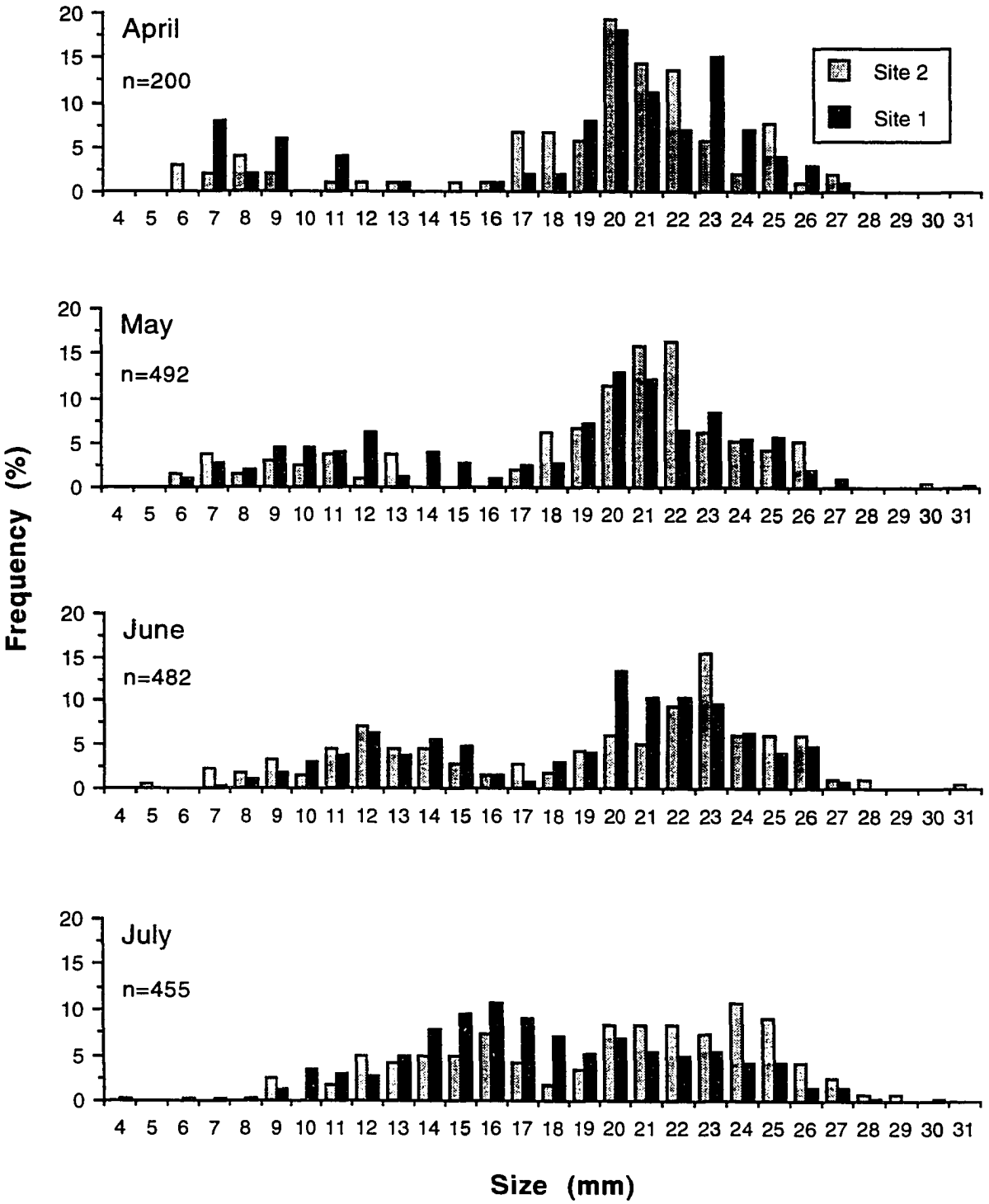

Figure 5.2: *Nucella lima* proportional size frequency at two locations in Kasitsna Bay during 1992.

laboratory experiment with a very small sample size (n=3 survivors), *Nucella lima* hatchlings that survived grew from an initial size of 1 mm at hatching to a 6-9 mm length after 12 weeks. In the spring (April), young snails in the field had a size mode of 7 mm (Fig. 5.2). By July, this cohort had grown to a modal size of 16 mm.

Average mussel size during the summer of 1993 was $26.7 \pm 0.95_{SE}$ mm (n=80) and mean density was 9460 m^{-2} (n=10 quadrats). In 1986, before the freeze, average length of mussels was 56.0 mm (n=816) with a mean density of 1900 m^{-2} (n=7 quadrats) (R.C. Highsmith, unpublished data). This indicates a shift in demographic characteristics of the mussel population caused by the freeze has been maintained for >3 years following that event.

In July 1992, mean *Nucella* density at the Kasitsna Bay sites was high ($131.6 \pm 15.6_{SE}$ m^{-2}; range = 56-200 m^{-2}), while the density at Nubble Point was significantly lower ($2.8 \pm 4.4_{SE}$ m^{-2}; range = 0-16 m^{-2}) (ANVOA: df=1,38, F=211.8, P<0.0001) (Fig. 5.3). In fact, there was no overlap between the *Nucella* density distributions at these two sites. Mussel cover varied inversely to *Nucella* densities at both Kasitsna Bay and Nubble Point. Mussel cover at Kasitsna Bay was less than half ($31.4 \pm 1.95_{SE}$%) that at Nubble Point ($72.4 \pm 2.5_{SE}$%) (ANVOA: df=1,58, F=127.7, P<0.0001) (Fig. 5.3). This inverse pattern suggests a negative effect of *Nucella* density on mussel abundance and is further supported by the strong negative correlation between *Nucella* density and mussel cover in individual quadrats (Fig. 5.4). The site-to-site pattern of predator and prey abundance is consistent with the expectation that high predation will regulate prey abundance.

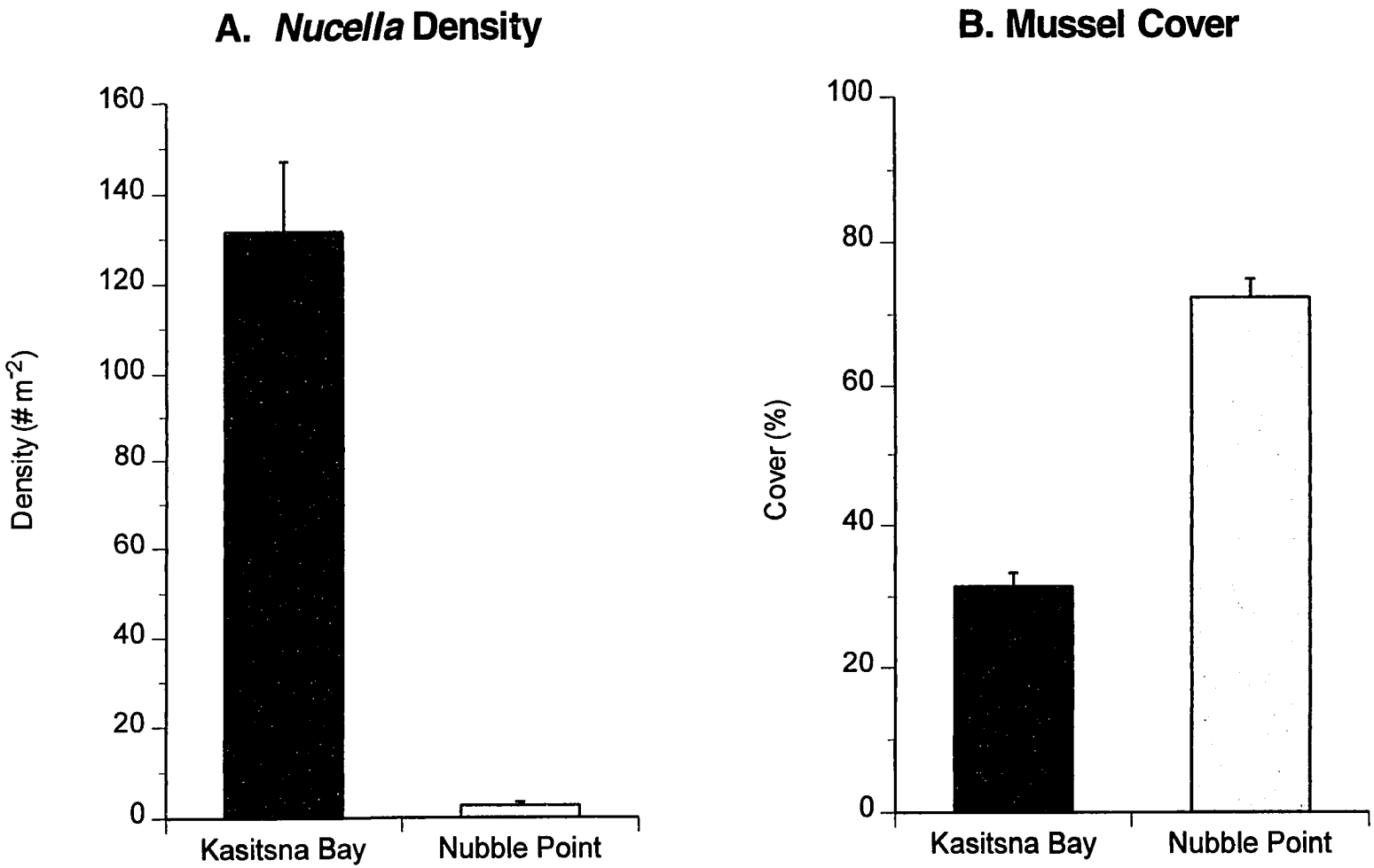

Figure 5.3: *Nucella* density (A) and *Mytilus* cover (B) at Kasitsna Bay and Nubble Point in July 1992 (±SE).

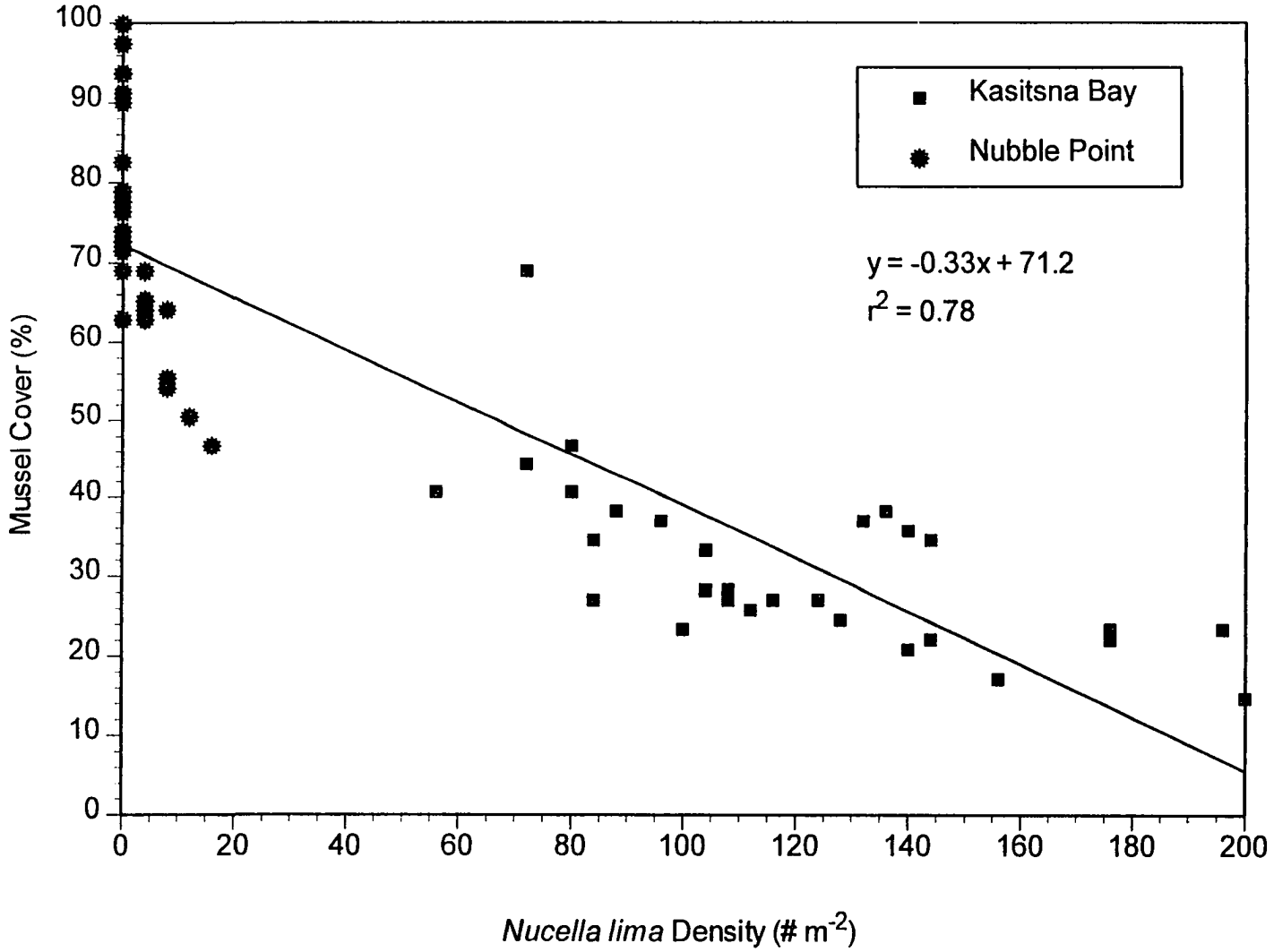

Figure 5.4: Mussel cover relative to *Nucella* density at Kasitsna Bay and Nubble Point.

Sources of Mussel Mortality

The impact of *Nucella* predation on mussels can be distinguished from other mortality sources by the distinctive hole drilled in the mussel shell during a feeding bout. At the Kasitsna Bay site, *Nucella* predation is clearly a major source of mortality for mussels, with about three-fourths of empty shells having drill holes (Fig. 5.5). Of course, this assessment cannot account for mortality sources, such as high waves or predation by gulls or ducks, which remove the entire shells from the site. However, the probability of such factors causing significant mortality is low as wave action in summer is relatively moderate and avian predators have not been observed taking mussels at the sites. In contrast, *Nucella* predation was negligible at Nubble Point (Fig. 5.5). Thus, where *Nucella* is abundant, mussel predation rates are correspondingly high.

Impact of *Nucella* on Mussel Beds

To reduce the cover of mussel populations under natural conditions, snails must eliminate mussels faster than the rate at which they increase cover by non-numerical means such as recruitment, growth, and migration. Mussels, especially smaller individuals, easily migrate short distances through action of a muscular foot and selective attachment of byssal threads. Mussels often move to free space at the edge of clumps or beds (Seed, 1976; Suchanek, 1979, 1986). In the caging study, *Nucella* density had a significant effect on mussel cover (repeated measures ANOVA: df=2,21; F_{RM}=13.98; P<0.0001) (Fig. 5.6). Both normal and high density *Nucella* treatments resulted in significantly reduced mussel cover (Table 5.1a), although the high density

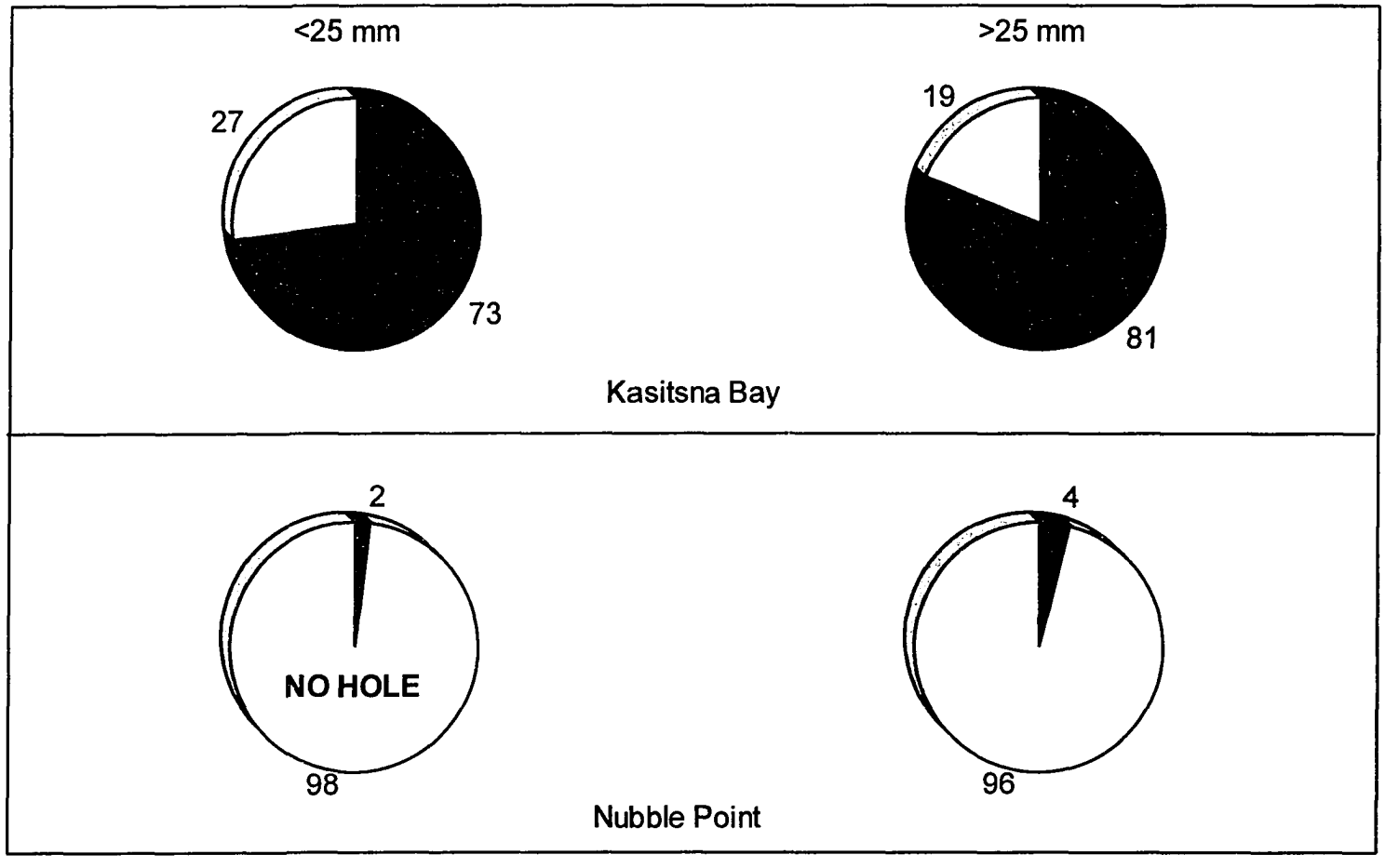

Figure 5.5: Proportion of small (<25 mm length) and large (>25 mm length) dead mussels at Kasitsna Bay and Nubble Point whose mortality was due to *Nucella* predation. Results are from observations on the first 100 empty shells in both size classes at each site.

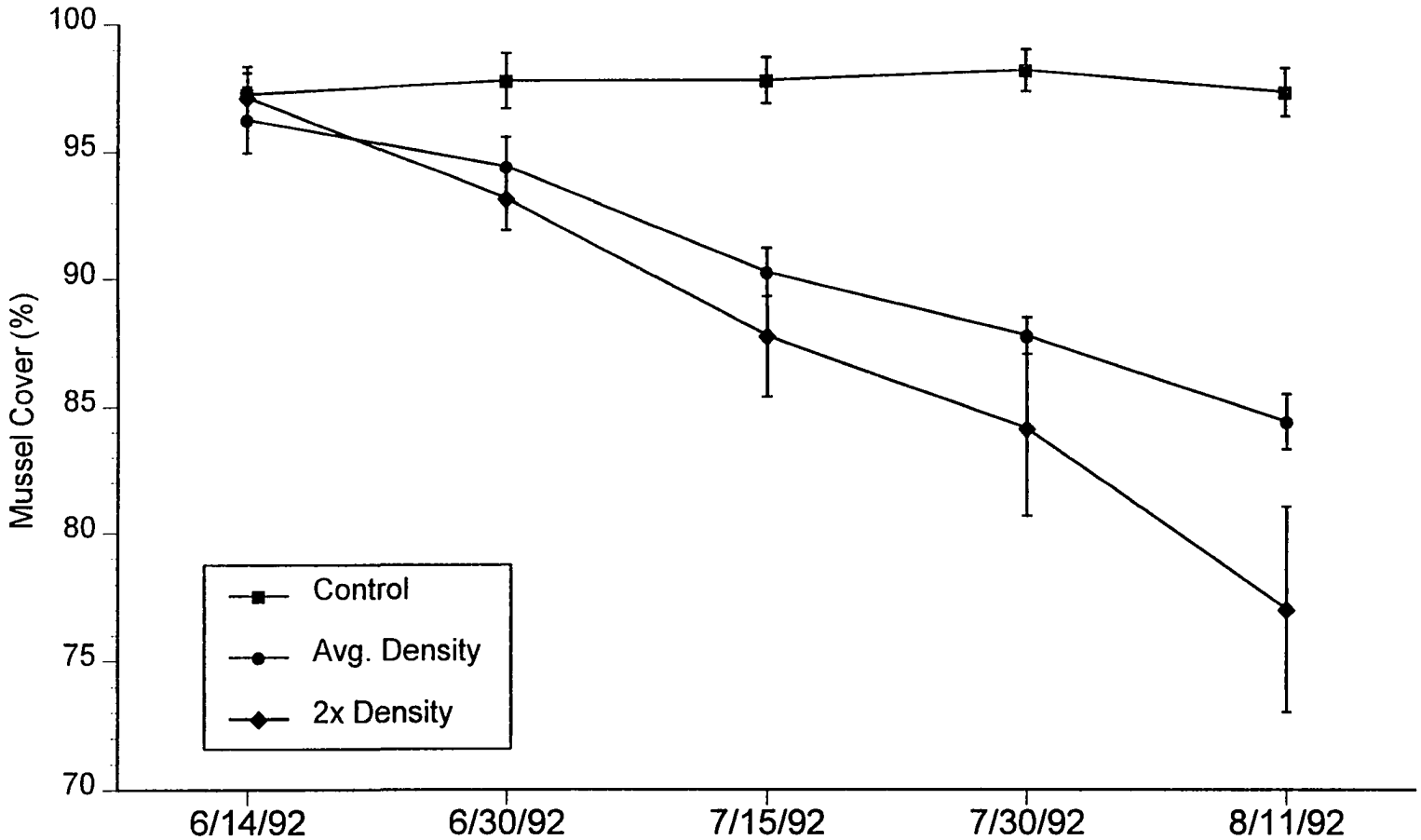

Figure 5.6: Mussel cover (±1 SE) through time as a function of *Nucella* density in caged arenas. There were 8 replicates per treatment. The Average Density treatment contained 5 snails and the High Density treatment contained 10 snails. Control arenas had no snails.

Table 5.1a: Initial and final *Mytilus* cover (% ±SE) containing zero (control), average and high densities of *Nucella lima* in 0.04 m^2 cages with 8 replicates per treatment. F-ratios and P-values are the result of one-way ANOVA. Data were subjected to an arcsine-square root transformation prior to analysis to normalize the distribution of percentage data.

	Control	Avg. Nucella Density	High Nucella Density	DF	F-ratio	P-Value
Initial	97.25 (1.09)	96.25 (1.29)	97.13 (0.95)	2,21	0.41	0.6664
Final	97.25 (0.94)	84.38 (1.08)	77.00 (4.01)	2,21	27.47	0.0001
DF	1,14	1,14	1,14			
F-ratio	0.01	42.55	36.38			
P-Value	0.9401	0.0001	0.0001			

Table 5.1b: Pairwise comparisons examining effect of zero (control), normal, and high densities of *Nucella lima* on mussel cover. Comparisons are made among all three predation levels on initial and final mussel cover, and significance groupings result from Tukey comparisons with an α error rate of 0.05.

	N	Initial		Final	
		Mean	Group	Mean	Group
Control	8	97.25 (1.09)	A	97.25 (0.94)	A
Average Density	8	96.25 (1.29)	A	84.38 (1.08)	B
High Density	8	97.13 (0.95)	A	77.00 (4.01)	B

treatment did not result in significantly greater reduction in cover of the mussel bed than the normal density treatment (Table 5.1b).

The initial mussel cover in the cages was so high (>90%) that snails did not have sufficient free space in which to rest or move about freely. During feeding events, which last many hours, snails sometimes became entrapped and incapacitated by byssal threads of mussels. This can lead to death of *Nucella* under some circumstances (Petraitis, 1987; Day *et al.*, 1991). Trapped snails were freed during censuses but their overall feeding efficiency was reduced. Therefore, the reduction in mussel cover observed in the two predation treatments is probably conservative (Fig. 5.6).

Discussion

Mytilus trossulus is usually a common and dominant space occupying species on rocky shores in Alaska (Feder *et al.*, 1977; Feder & Keiser, 1980; O'Clair & Zimmerman, 1987) and occurred locally in high densities in Kachemak Bay prior to the freeze (R.C. Highsmith, unpublished data). Although *M. trossulus* can withstand a wide range of environmental variability including freezing temperatures (Seed, 1976; Suchanek, 1978; personal observation), it was not able to survive the effects of unusually low temperatures during a spring tide series that occurred in southcentral Alaska during January 1989.

The disparate difference in *Nucella* density between summer and winter (Fig. 5.1), combined with the age structure of the *Nucella* population (Fig. 5.2)

suggests that, during the winter, snails migrate lower in the intertidal, probably to avoid increased wave action and colder temperatures.

As a result of mussel mortality and subsequent removal, space made available was colonized within 4 months by a heavy barnacle set which, often filled >95% of primary space throughout the former *Mytilus* zone (Chapter 3, Fig. 3.3). Hence, the immediate effect of this disturbance event was a shift in community structure resulting from the removal of the dominant space occupier.

Despite intense predation pressure on mussel populations, established beds of adult mussels can typically persist because of high fecundity, regular recruitment, high growth rates, and relatively long life-spans. Size and space refugia may also allow mussels to coexist with predators (Dayton, 1971; Paine, 1976; Seed & Brown, 1978; Pollock, 1979; C.L. Griffiths & Seiderer, 1980; R.J. Griffiths, 1981). In this study, discontinuous beds of large mussels which survived the freeze usually occurred lower in the intertidal than the younger individuals, and would presumably be more available to attacks by *Nucella* due to increased foraging times. Although *N. lima* is physically capable of feeding upon large, adult mussels (R.C. Highsmith, unpublished data), the established mussel beds did not seem adversely impacted by predation, as adult mussel beds persisted throughout this study despite high predator densities (Fig. 3.5; personal observation). However, mussel populations composed of younger, smaller individuals higher on the shore have been unable to increase their occupation of space in the presence of high *Nucella* densities.

The observational and experimental results of this study show variation in *Nucella* density between sites and demonstrate an inverse correlation between predator density and prey abundance. In the field, *N. lima* is capable of significantly reducing prey densities. Where snails are abundant, they are responsible for a large proportion of the mortality of their prey. At these sites, mussel populations were unable to increase their spatial occupation. However, where *Nucella* is rare and resulting predation pressure is low (e.g. Nubble Point) mussels were a dominant spatial component of the community. Although no supporting data exist, presumably mussel populations at Nubble Point were exposed to the same environmental extremes during the January, 1989 freeze as other sites. Therefore, mussel populations at Nubble Point likely suffered losses comparable to other sites. As a result, the dense mussel cover at Nubble Point in 1992 was probably composed of individuals which arrived after 1989, indicating the success of mussels in recovering from a major disturbance when released from heavy predation pressure.

Seed (1976) reported laboratory consumption rates for adult *N. lapillus* feeding on *M. edulis* (10-30 mm in length) in the laboratory of 2.17 mussels week^{-1}. Extrapolating Seed's data to the present study with predator densities at Kasitsna Bay of ≅125 snails m^{-2} and prey density of 9460 mussels m^{-2} (n=10), then *N. lima* could successfully prey upon 87% of all individuals in a continuous mussel bed after 30 weeks of feeding. Based on the rate of reduction of mussel cover induced by snails in the fenced feeding trials at Kasitsna Bay, estimated reduction in the mussel population during a 30 week period would be 58%. However, this latter estimate probably

represents a minimum boundary because some of the *Nucella* became trapped among mussel byssal threads and were unable to forage until released. Furthermore, mussels at the Kasitsna Bay site occur in small patches and their resulting cover is much lower than 100% used in the above estimates. Hence, predation by *N. lima* may exert even greater influence on individual patches than the calculated 60-90% reduction in mussel populations over the course of one feeding season. These estimates of predation rates underscore the potential impact on the mussel population by *N. lima* and, therefore, demonstrates an effective mechanism of predator control of prey populations in this community. This result contrasts with Hughes' (1980) generalization that increased physical harshness of the environment seems to be correlated with the diminished importance of predation in affecting community structure. In Alaska, physical extremes are clearly greater than in most temperate regions, yet this study demonstrates effective predator control of a prey population.

Although mussel recovery rates may vary with several factors including timing of the disturbance and spatial extent of the disturbed patch, the recovery of mussels from disturbance is considered to be deterministic (Paine & Levin, 1981; Suchanek, 1981, 1986; Paine, 1984). For example, in New England, Lubchenco & Menge (1978) demonstrate that mussel beds on exposed shores are highly susceptible to removal by winter storms. However, settlement processes, high growth rates, and superior competitive ability usually led to mussel dominance by the end of the summer following removal. This cycle, they suggest, is more or less an annual event and

emphasizes how rapidly mussels may recover from disturbance and monopolize large expanses of intertidal substrate.

In contrast to New England, a lack of predictable spatial dominance by mussels over a 3 year period at sites of high *Nucella* density is apparent in the present study. In addition to reductions in mussel cover which are highly correlated with predator density (Fig. 5.4, 5.6), demographic characteristics of mussel populations where predators are abundant remain altered compared to pre-freeze levels, as mean mussel size during 1993 was less than half that in 1986 (26.7 mm vs. 56.0 mm).

Other factors could potentially affect recovery of *Mytilus* populations. Lack of appropriate filamentous species which *Mytilus* utilizes for primary settlement, lack of sufficient numbers of adults in the region necessary to provide an adequate pool of larvae, and slow growth at high latitudes are alternate explanations for the failure of mussels to regain spatial dominance. However, none seem to be important in this study. First, the slow mussel recovery does not seem to be due to the lack of suitable locations for initial or secondary settlement. On the contrary, the community composition prior to mussel recruitment consisted of heavy barnacle cover, and filamentous algae was also common. Bare rock surface was rare (see Chapter 3). Second, populations of mussels survived in the lower intertidal zones so there was a local source of propagules. Moreover, mussel larvae are planktotrophic and are therefore capable of long-distance dispersal, so local recruitment may be driven by propagules released by adults a great distance away. Also, mussel recruits were common throughout the summer months (Fig. 3.5). So the failure of mussels to gain spatial dominance does not seem to result from

lack of recruitment. Third, slower growth resulting from cooler temperatures and seasonal extremes associated with the high latitude may be a factor. However, Kachemak Bay is one of the worlds most productive coastal ecosystems (see Chapter 2) and therefore food limitation is unlikely. Although growth rates of individuals could be reduced by the cool temperatures, the mussel population as a whole achieved spatial dominance at sites where predators are rare. Thus, slow growth does not appear to be an important factor limiting mussel recovery in Kachemak Bay.

The importance of physical forcing functions in affecting community structure through alteration of predator-prey interactions has been elegantly developed in a series of papers examining community structure in New England (Menge, 1976, 1978a,b, 1983; Lubchenco & Menge, 1978; Menge & Lubchenco, 1981). At locations protected from heavy wave action, predators significantly influenced the lower limit of *M. edulis* distribution. In locations exposed to heavy wave action, predator densities were reduced, making them ineffective at controlling mussel densities, so *M. edulis* achieved long-term spatial dominance. In New England, instead of a stochastic, severe disturbance event as in this study, the physical forcing function was deterministic and chronic and varied along a predictable gradient (from low to high exposure).

In the present study, a severe freeze influenced the community through differential mortality of constituent species. This event altered the balance between mussel population losses due to predation, principally from *N. lima*, and increases due to recruitment and growth. Thus, predator control of

mussel populations in this situation was made possible by a rare catastrophic physical disturbance.

In Kachemak Bay, heavy winter kill and locally intense predation pressure have combined to control mussel densities. By eliminating large numbers of adults which may have provided shelter from predators and wave action, a physical disturbance event facilitated predator control of mussel populations. Also, the site-specific predation rate probably increased as *Nucella lima* likely fed upon more younger, smaller individuals. Because the freeze was acute and unpredictable, it may not be considered as a mechanism of prey population regulation, but its influence on the structure of the local community, not only in direct initial effects but also in mediating a significant predator-prey interaction, is clear.

SUMMARY

The post-freeze predator-prey interactions between mussels and snails were studied to examine the effect of predation by *Nucella* on the recovery of *Mytilus* populations. Subsequent to the freeze, mussel populations recovered at Nubble Point where *Nucella* was rare. However, at Kasitsna Bay, where *Nucella* densities were consistently high (>100 m^{-2}), mussel cover remained significantly lower. At the latter sites, as much as 81% of mussel mortality was due to snail predation. In some microhabitats low in the intertidal, mussels survived the freeze and persisted despite high predator densities. These patterns of mussel population dynamics and experimental evidence presented in this paper indicate that young mussels are effectively controlled

by intense predation by *Nucella*. However, mussels may have a refuge in size from significant predator-induced mortality, even where predators are found in high densities. Hence, a stochastic, catastrophic disturbance event influenced the structure of this community by removing dense stands of large prey individuals that had grown to a refuge size. The disturbance thus facilitated long-term *Nucella* control of mussel-dominated communities by shifting the balance of *Nucella-Mytilus* interactions toward smaller prey individuals more susceptible to *Nucella* predation.

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CHAPTER 6

ROLE OF BARNACLES IN *FUCUS GARDNERI* RECRUITMENT

INTRODUCTION

Species-specific chemical cues that induce settlement in pelagic larvae of benthic species are widespread in the marine environment (Crisp, 1984; Pawlik, 1992). Most benthic marine invertebrate species have a multi-phasic life cycle which includes a planktonic larval phase (Thorson, 1950, 1964; Roughgarden *et al.*, 1988). Dispersal via planktonic larvae is an important mechanism for maintaining genetic diversity and minimizing local extinction for fixed or sedentary benthic invertebrates (Strathmann, 1974; Crisp, 1979), despite the high levels of mortality associated with such a journey (Thorson, 1966; Day & McEdward, 1984; Young & Chia, 1987). Larvae spend anywhere from minutes to months as meroplankton and may disperse distances ranging from meters to hundreds of kilometers from their origin (Thorson, 1950, 1961; Scheltema, 1971a,b; Pawlik, 1992).

Larvae have little control over where they are transported on large scales (Butman, 1987), as larval swimming rates are insignificant compared to oceanic transport processes (Okubo, 1971; Levin, 1983, Chia *et al.*, 1984; Farrell *et al.*, 1991). On small spatial scales, however, larvae exhibit behaviors which result in non-random settlement patterns (e.g. Meadows & Campbell, 1972; Crisp, 1974; Scheltema, 1974; Chia & Rice, 1978; Highsmith, 1982; Keough & Downes, 1982; Wethey, 1984, 1986; Butman, 1987). Indeed, larvae often exhibit a remarkable specificity for favorable microhabitats in which to settle. Because the suitability of the settlement site undoubtedly has a profound effect on the ultimate success of an organism (Lindner, 1984), any behavior that a larva can employ to locate a favorable

settlement site should confer an advantage to its survival, and therefore should enhance its fitness.

Although physical properties of the substratum have been shown to influence micro-settlement patterns of larvae (Gray, 1974; Ryland, 1974; Crisp, 1984; Wethey, 1986; Wethey *et al.*, 1988; Raimondi, 1988, 1990; Hodgson, 1990; Walters & Wethey, 1991), physical aspects likely are secondary in importance to chemical characteristics of a potential settlement site (Mihm *et al.*, 1981; Le Tourneaux & Bourget, 1988; Pawlik, 1992). Larval response to chemical cues has been demonstrated in numerous taxa in a diversity of phyla including coelenterates (Williams, 1965; Chia & Bickell, 1978), annelids (Williams, 1964; Cuomo, 1985), molluscs (Crisp, 1967; Bayne, 1969; Hidu, 1969; Veitch & Hidu, 1971; Morse & Morse, 1984), echinoderms (Strathmann, 1978; Highsmith, 1982), arthropods (Knight-Jones, 1953; Crisp & Meadows, 1962, 1963; Crisp, 1984; Yule & Walker, 1984), and ascidians (Cloney, 1978). Responses can occur in relation to cues generated by adult conspecifics (gregarious settlement), adults of other species (associative settlement [sensu Crisp, 1974]), or cues generated by geochemical reactions in the sediment (Cuomo, 1985).

Perhaps the best studied larval-adult interaction (gregarious settlement response) via chemical cues involves the intertidal barnacle *Semibalanus balanoides* (reviews by Crisp, 1984; Gabbott & Larman, 1987; Pawlik, 1992). Barnacle cyprids competent to settle exhibit a strong response to a chemical factor present in both the tissues and test of adult barnacles (Knight-Jones, 1953; Crisp & Meadows,1962). The settlement factor was found to be water soluble, but only elicited a response when it was adsorbed to a surface (Crisp

& Meadows, 1963). The active fraction of the settlement factor was isolated and identified as a closely related group of proteins, with subunits of 5,000-6,000 and 18,000 daltons (Gabbott & Larman, 1971; Larman & Gabbott, 1975, Larman *et al.*,1982; Larman, 1984), and found in all arthropod cuticles (hence the name arthropodin; Fraenkel & Rudall, 1940).

Fucoid macroalgae are a conspicuous space occupant on upper and middle level temperate rocky intertidal shores throughout the northern Atlantic and Pacific Oceans (Stephenson & Stephenson, 1972; Lubchenco, 1980, 1983; Hawkins, 1981; Van Alstyne, 1988; Chapman, 1989; Vadas *et al.*, 1990; Ang, 1991a,b, 1992; Ang & De Wreede, 1992; Arrontes, 1993). Fucoids are an important structural component of temperate rocky intertidal communities, not only because they often occur in high densities, but also because a dense fucoid canopy often influences the intertidal environment by moderating extremes in physical variables such as wave action, temperature, and desiccation (Brosnan, 1990; Brawley & Johnson, 1991; McCook & Chapman, 1991).

Fucus gardneri is a conspicuous space dominant in southcentral Alaska, typically occupying a large portion of the substrate on upper level shores and often forming dense canopies (this study, Chapter 3). Its vertical distribution in the intertidal zone overlaps extensively with the high-shore barnacles *Semibalanus balanoides* and *Balanus glandula*, which are often considered ecological equivalents in Alaska (O'Clair & Zimmerman, 1987). Reproduction in *Fucus gardneri* involves the release of fertilized eggs from conceptacles located on the tips of reproductive thalli (receptacles) into the water (Callow *et al.*, 1985; Ang, 1991a; Ang & De Wreede, 1992) during much of the

summer. Dispersal is usually limited, as propagules sink relatively quickly and adhere to the substrate surface (Lobban *et al.*, 1985).

The *EXXON VALDEZ* oil spill in March 1989 resulted in heavy losses of *Fucus* in the mid- to upper-intertidal zone (Stekoll *et al.*, 1993; van Tamelen & Stekoll, 1993). *Fucus* was slow to recover, especially on open rock surfaces where barnacles had also succumbed to the oil spill or subsequent clean-up activities. In non-oiled locations of southcentral Alaska, *Fucus* succumbed to a severe freeze in January, 1989. However, *Fucus* readily recolonized at these sites, which often contained high densities of barnacles (Chapter 3, this study). These observations suggested that an investigation of the factors influencing *Fucus* recruitment might yield new information about *Fucus'* ability to recover from acute disturbances.

This study examines *Fucus* recruitment dynamics by determining how existing barnacle cover influences patterns of *Fucus* recruitment. Enhancement of macroalgal recruitment, including *Fucus spp.*, by existing barnacle cover has been documented by a number of researchers (Burrows & Lodge, 1950; Choat, 1977; J.L. Menge, 1975; Lubchenco & Menge, 1978; Lubchenco, 1980, 1983; Hawkins, 1981; Norton & Fetter, 1981; Jernakoff, 1983; Chapman, 1989). The mechanism of enhanced *Fucus* recruitment has been suggested to result from the increased rugosity provided by crevices between barnacles. This structural heterogeneity apparently protects germlings from desiccation stress and limits the effectiveness of grazers by creating grazer-free refuges. However, the only specific experimental test of this hypothesis revealed that *Fucus* recruitment success was not dependent on the activities of consumers (Chapman, 1989).

In this paper, the results of field experiments are reported which demonstrate enhanced *Fucus* recruitment in the presence of barnacles. However, the observed recruitment patterns, rather than resulting from the physical characteristics of the substratum created by barnacles, are instead consistent with the hypothesis that *Fucus* eggs are stimulated to attach in response to a chemical cue, possibly produced by barnacles to attract conspecific larvae. Further, a probable mechanism by which a non-motile plant egg such as *Fucus* may respond to a chemical cue was investigated. Although chemical cues produced by one species commonly elicit behavioral responses from other species, this is the first demonstration of a response of a plant propagule to a chemical cue produced by an animal species.

METHODS

A combination of field and laboratory studies were conducted to determine whether live barnacles or barnacle shell structure enhance or facilitate recruitment of *Fucus gardneri*.

Field Studies

Two sites were chosen to examine the factors affecting *Fucus* recruitment: Kasitsna Bay and Nubble Point. These sites differed in their exposure to wave action and existing *Fucus* cover (Nubble Point > Kasitsna Bay for both). Quadrats (0.25 m^2) were located at each site in the center of *Fucus*' vertical distribution (+3.0 to +4.0 m) in microhabitats where existing *Fucus* cover was relatively high and adult plants appeared healthy and vigorous. This placement insured that the specific locations chosen were favorable sites for

Fucus colonization and provided the greatest chance of a ready supply of propagules available for recruitment.

The corners of each quadrat were permanently marked with stainless steel screws secured in plastic wall anchors imbedded in holes drilled in the rock. In April 1992 at Kasitsna Bay, three treatments were established in a randomized block design, each with three replicates, to determine how factors associated with existing barnacle cover affected *Fucus* recruitment. Treatments were: live barnacle cover, barnacle structure (empty tests only), and a control cleared of all barnacles and shell structure. The structure (hereafter referred to as tests only) treatment was established to discern physical effects associated with barnacle shells, such as hydrodynamic eddies causing passive depositional areas (Eckman, 1983; Hannan, 1984; Wethey, 1986; Butman, 1987; Wethey *et al.*, 1988; Walters & Wethey, 1991) or cracks and crevices on or between barnacle tests (Jernakoff, 1983; Lubchenco, 1983).

Existing *Fucus* was removed from the quadrats and in a 10 cm buffer zone around quadrats by cutting plants as close to the holdfast as possible. No regeneration from existing holdfasts was observed during the course of this study. The test only treatment at Kasitsna Bay was created by killing live barnacles by inserting a sharp probe through the aperture. Control quadrats were cleared mechanically of all existing macro-organisms.

In June 1992, quadrats were established at Nubble Point in the same design and using the same procedure described above, with one exception. Barnacle cover in the Nubble Point quadrats was greater than at Kasitsna Bay (Nubble Point = $63.2 \pm 3.6_{SE}$%; Kasitsna Bay = $48.8 \pm 7.0_{SE}$%; ANOVA:

n=6, df=1, F=7.83, P=0.02). Hence, sacrificing barnacles individually with a probe for the test only treatment seemed prohibitively time consuming. Therefore, barnacles at Nubble Point were killed in place by heating them with a propane torch.

Cover of barnacles, barnacle tests and *Fucus* was determined in the quadrats by overlying the quadrat with a frame, using the corner screws for alignment. The frame contained a crosshatch grid of 81 points (every 5 cm on both axes). The category of organism directly under each point was recorded. Cover was determined as the proportion of points directly over each cover group compared to the total number of points in the grid. Quadrats were censused monthly during the summer of 1992, once during the winter of 1992-1993, and again monthly during the spring and summer of 1993.

In January 1993, after preliminary results revealed differences in patterns of *Fucus* recolonization in the structure only treatments at the two sites, additional quadrats were established at Nubble Point. This auxiliary experiment was designed to directly compare *Fucus* recolonization in test only quadrats created by the poking and torching methods.

Three replicate pairs of quadrats were established, with each quadrat of a pair located directly adjacent to the other. Existing *Fucus* was removed as described above. All barnacles in one quadrat in each pair were killed using the poking method, while the barnacles in the other quadrat were torched. Cover was estimated as described above.

Data collected in this experiment could not be considered independent nor could a normal distribution of the data be assumed, because the same

quadrats were censused repeatedly to determine patterns of recolonization and because of the low level of replication within each treatment (n=3), respectively. Differences in the magnitude of recruitment between treatments were compared using the distribution-free Wilcoxon Sign-Rank Test, and comparisons of the same experimental treatment between sites were made using a Kruskal-Wallis test (Segal, 1956; Sokal & Rohlf, 1981). All data analysis was conducted using PC-SAS, version 6.04 (SAS, 1988).

Laboratory Studies

Experiments were conducted with *Fucus* embryos in the laboratory to resolve on a finer scale the process by which *Fucus* eggs attach to the substrate and the factors which may influence the attachment process and subsequent growth of *Fucus* germlings.

To obtain fertilized embryos, mature, whole plants were collected from the shore. Receptacles are located at the distal ends of the thalli. The most fertile receptacles are inflated at the tips of the thalli and dark, opaque conceptacles can be observed when the receptacle is backlit. Whole plants were dried at ambient temperatures for 24 hours after collection. Receptacles were then excised from the plants and placed in small jars containing 4°C seawater. This cold stressing procedure caused conceptacles to open and embryos to be released. The receptacles were removed from the jars after 1 hour and the jars allowed to warm to room temperature.

Following observations to determine characteristics of newly released *Fucus* eggs, experiments were conducted to determine the effect of factors

on the settlement and attachment of *Fucus* eggs. These included the effect of surface-adsorbed barnacle extract on the strength of adhesion of *Fucus* eggs to a surface was examined. Test surfaces used were 14 x 14 cm plates made of 0.32 cm-thick Lexan plastic. The smooth plastic surface was roughened systematically with coarse sandpaper (36 grade). The plates were treated with the crude extract of whole barnacles, sans tests (Yule & Crisp, 1983). Treated plates were air dried completely to the touch and briefly rinsed in seawater before use.

Fertilized *Fucus* eggs were obtained with the method described above and used in all experiments within 48 hours of their release from conceptacles. Both control and treatment plates were seeded with *Fucus* eggs in 0.5 to 1 ml of seawater pipetted from the spawning jars, with an initial density goal of 50-100 eggs cm^{-2}. An attempt was made to seed all plates (replicates and treatments) from the eggs of a single receptacle (=spawning jar). When this was not possible due to low egg density, eggs from a second jar spawned at the same time using a receptacle from the same plant were used. In no cases were different eggs used for different treatments of the same replicate. On each plate, seeding was conducted in a 9 cm^2 permanently marked grid in the center of the plate. Once seeded, the eggs were left undisturbed on the plate in the original seawater medium for 1 hour, then placed in seawater (non-flowing) overnight (12 hours). Plates were rinsed gently, and the eggs attached to the center 1 cm^2 area were counted.

Seeded plates were then subjected to trials of flowing seawater at three different velocities in an attempt to determine the proportion of eggs attached on treated and untreated surfaces. After initial counting, plates were exposed

to a low flow trial (approx. 20 cm sec^{-1}) for 15 sec, then were recounted before being exposed to the moderate flow level (approx. 40 cm sec^{-1}), and were again counted for eggs remaining before the final trial in high flow conditions (approx. 60 cm sec^{-1}). These data were analyzed by one-way analysis of variance to test for effects of surface treatment on resistance to dislodgement by water flow (= strength of adhesion).

RESULTS

Fucus Recruitment in the Field

Fucus recruitment in 1992 at both Kasitsna Bay and Nubble Point was greater in the live barnacle treatment than the test only treatment, while there was virtually no response in the cleared control (Fig. 6.1; Table 6.1A). Site-to-site comparison of recruitment in the live barnacle treatment reveals *Fucus* recolonized the live barnacle treatment at Nubble Point site more rapidly and to a greater overall magnitude than at Kasitsna Bay, even though quadrats at Nubble Point were established two months after those at Kasitsna Bay (Fig. 6.1).

Based on the inter-site recruitment patterns in the live barnacle treatment, the expectation would be that the structure only treatment would also show greater recruitment at Nubble Point than at Kasitsna Bay. However, the actual pattern initially exhibited the opposite trend. Although mean *Fucus* recruitment in the test only treatment at both sites was much lower than in the live barnacle recruitment (Fig. 6.1), the test only treatment at Kasitsna Bay exhibited higher recruitment through January 1993 than at Nubble Point

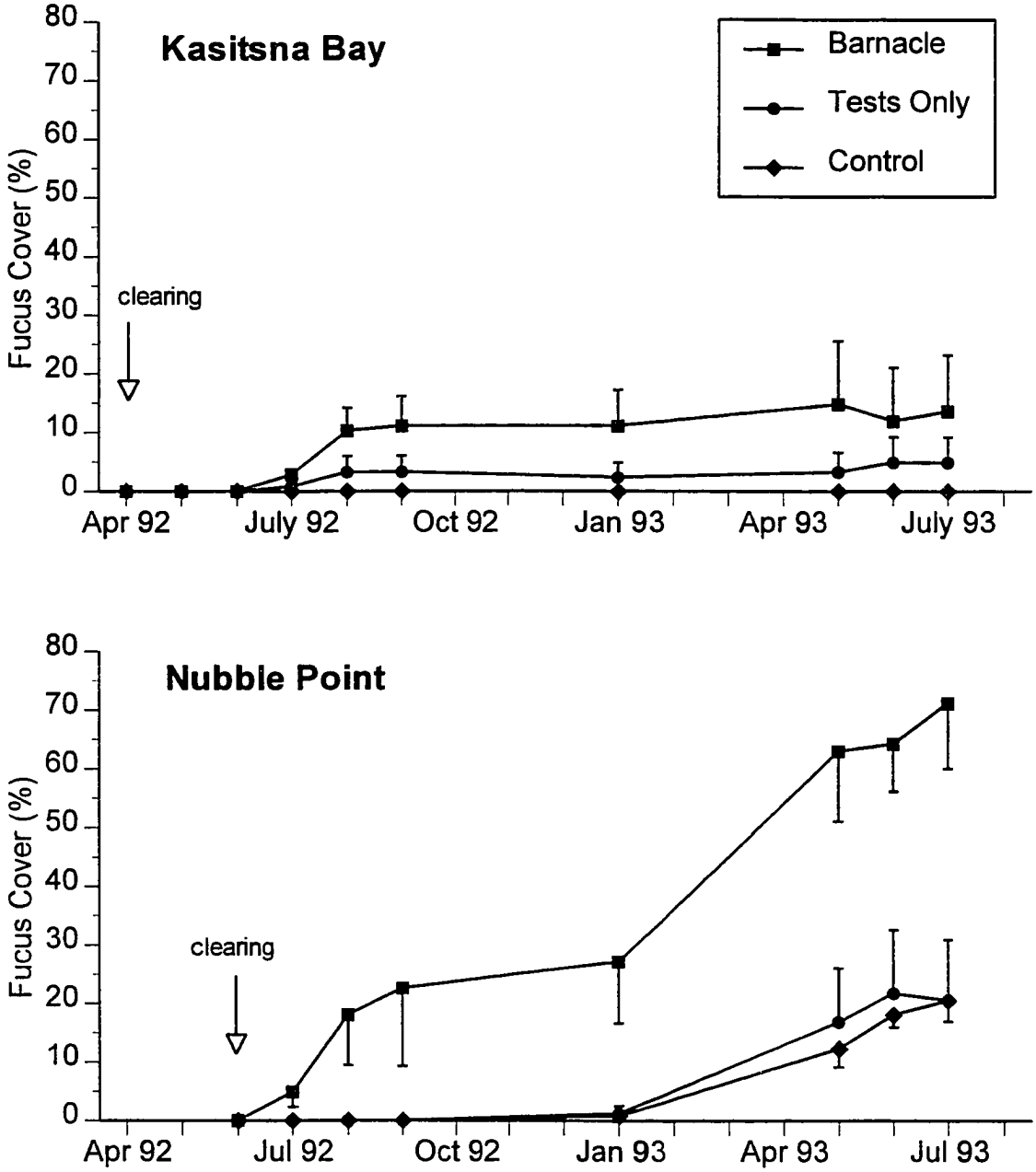

Figure 6.1: Mean *Fucus* cover (± SE) in quadrats initially cleared of existing *Fucus* plants. Quadrats were randomly assigned to one of three substrate cover treatments: live barnacles, empty barnacle tests, or cleared control. N=3 quadrats per treatment. The test only treatments were created using different methods at Kasitsna Bay and Nubble Point (see text).

Table 6.1: *Fucus gardneri* cover (%±SE) in recruitment quadrats in January 1993 (A) and July 1993 (B). *Fucus* was initially cleared from the Kasitsna Bay and Nubble Point quadrats in April and June 1992, respectively. Statistical values are the result of a non-parametric Wilcoxon Sign-Rank test testing for differences in *Fucus* cover between treatments.

A. JANUARY 1993

Site	Treatment	Fucus Cover (SE) January 1993	Wilcoxon Sign Rank Test			
			N	DF	CHISQ	P- value
Nubble Pt.	Live Barnacle Tests Only Control	27.2 (10.5) 1.2 (1.2) 0.8 (0.4)	12	2	23.59	<0.0001
Kasitsna Bay	Live Barnacle Tests Only Control	11.1 (6.1) 2.5 (2.5) 0	12	2	22.97	<0.0001
Both Sites	Live Barnacle Tests Only Control	19.1 (6.5) 1.9 (1.3) 0.4 (0.3)	24	2	45.05	<0.0001

B. July 1993

Site	Treatment	Fucus Cover (SE) July 1993	Wilcoxon Sign Rank Test			
			N	DF	CHISQ	P- value
Nubble Pt.	Live Barnacle Tests Only Control	71.2 (11.3) 20.6 (10.4) 20.6 (3.6)	21	2	21.09	<0.0001
Kasitsna Bay	Live Barnacle Tests Only Control	13.6 (9.6) 4.9 (4.3) 0	21	2	30.74	<0.0001
Both Sites	Live Barnacle Tests Only Control	42.4 (14.5) 12.8 (6.1) 12.3 (4.9)	42	2	38.87	<0.0001

(Kruskal-Wallis test; n=12, df=1, Chisq=4.66; P=0.03). By the summer of 1993, *Fucus* cover at Nubble Point had continued to increase in the live barnacle treatment, but recruitment had substantially accelerated in the control and test only treatments (Fig. 6.1; Table 6.1B). This pattern was likely caused by natural alteration of the test only and control treatments over the autumn and winter of 1992-1993. Winter wave action had removed much of the existing shell structure from the test only treatment. Both the control and test only treatments had increased cover of live barnacles ($25.10 \pm 4.64_{SE}$%, n=3) resulting from growth of barnacles which recruited late in the previous summer. As barnacle recruitment and growth proceed, the difference between treatments should diminish and *Fucus* cover eventually converge. In both 1992 and 1993, patterns of *Fucus* recruitment in the test only treatment at Nubble Point closely followed those of the control treatment, while at Kasitsna Bay, these treatments exhibited somewhat different patterns relative to each other (Fig. 6.1).

Fucus recruitment in the auxiliary quadrats established at Nubble Point in January 1993 exhibited a clear trend which clarified the recruitment patterns in the1992 quadrats. The test only treatment that was poked, a method which left the chemical nature of the barnacle test intact, resulted in *Fucus* recruitment 10-fold greater than the treatment established by heating barnacles (Fig. 6.2; Table 6.2). The torched quadrats exhibited the same physical and structural characteristics as the poked treatment, but differed from the poked treatment chemically, as the extreme heat would have denatured any proteins and peptides in the organic matrix of the barnacle test. This result eliminates structural characteristics of the habitat due to

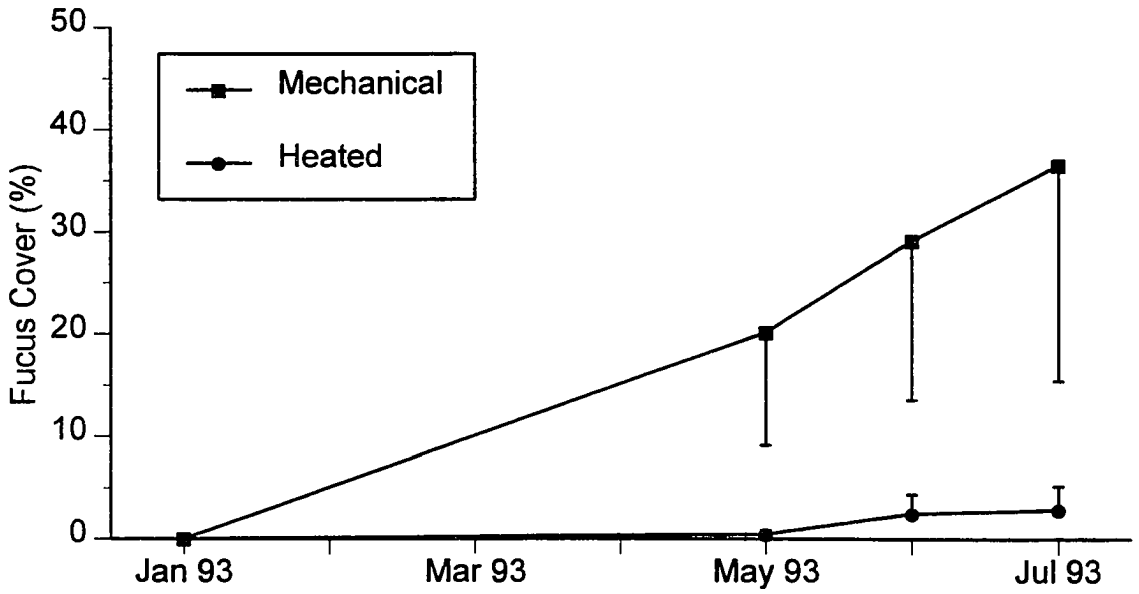

Figure 6.2: Mean *Fucus* cover (±SE) at Nubble Point in auxiliary quadrats initially cleared of existing *Fucus* plants in January 1993. Treatments reflect the method used to sacrifice the barnacles in paired quadrats.

Table 6.2: *Fucus gardneri* cover (%±SE) in auxiliary experiment established in January 1993 at Nubble Point. Treatments indicate the manner in which barnacles were sacrificed. Statistical values result from a Wilcoxon Sign-Rank test testing for differences in *Fucus* cover between treatments.

Treatment	Fucus Cover (SE) July 1993	Wilcoxon Sign Rank Test			
		N	DF	CHISQ	P- value
Mechanical Heated	36.62 (21.1) 2.9 (2.3)	9	1	12.07	0.0005

barnacle shells as a major contributing factor in *Fucus* recruitment because *Fucus* did not recruit to empty tests which were chemically, but not structurally altered; *Fucus* recruitment was significantly greater in the treatment in which tests were not chemically altered.

Fucus Attachment in the Laboratory

The absolute proportion of eggs remaining on plates differed between trials (ANOVA: n=27, df=1, F=6.12, P=0.02) and with flow regime (ANOVA: n=9, df=2, F=17.1, P<0.0001), but there was no statistical effect of surface treatment on egg tenacity (Trial 1: n=9, df=1, F=1.05, P=0.32; Trial 2: n=27, df=1, F=2.67, P=0.11). Although strength of adhesion between surface treatments was statistically similar, barnacle extract treated surfaces consistently exhibited a lower proportion of eggs remaining than untreated (control) surfaces (Fig. 6.3).

A possible reason for this negative result may involve the extraction technique used. The laboratory facility used during the experiments is at a remote location and did not have the equipment needed to properly filter and purify the crude extract of whole barnacles. While crude extract has been shown to elicit a response in barnacle cyprids (Yule & Crisp, 1983), it is entirely possible that the extract and surface preparation in this study resulted in anomalous behavior of the *Fucus* eggs. It was observed that the surface treatment failed to stay adsorbed to the plate surfaces. In fact, visible parts of the extract were observed sloughing off the plate surface during the trials. If the eggs were attached to these portions of the extract which readily sloughed off, then egg attachment would be negatively affected by this

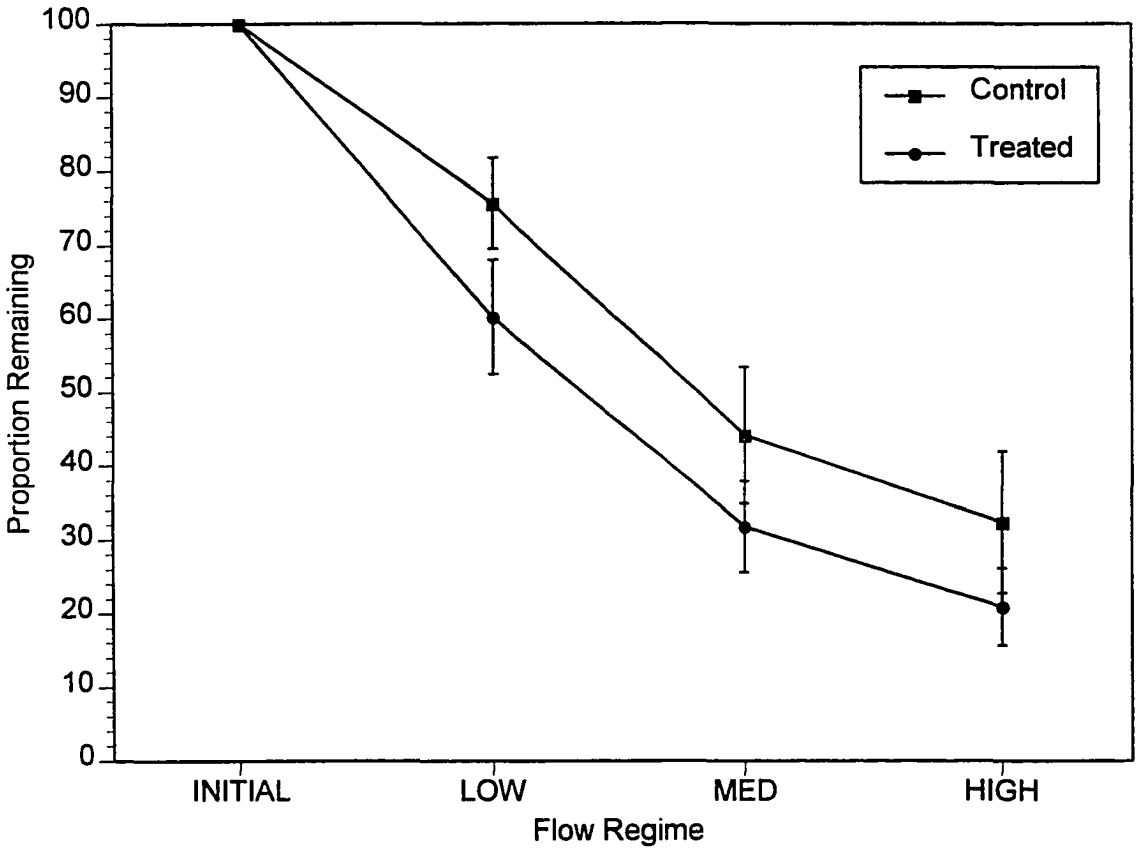

Figure 6.3: Comparison of *Fucus* eggs remaining on barnacle extract treated and untreated surfaces with increasing water flow (20, 40, and 60 cm sec^{-1} in low, medium, and high flow, respectively).

laboratory artifact. Therefore, although no treatment effect was observed, this could be in part or entirely due to problems associated with preparation of the extract plates.

Discussion

Fucus exhibited non-random recruitment patterns that cannot be explained by physical characteristics of the substratum but which are consistent with the 'chemical cue hypothesis' that *Fucus* eggs are stimulated to attach in response to a chemical cue associated with intertidal barnacles. Live barnacles clearly induced greater *Fucus* recruitment than barnacle tests only and cleared controls. Within the test only treatment, *Fucus* exhibited variation in recruitment depending on the manner in which the treatment was initiated. Treatments in which barnacles were killed using a procedure that left the chemical nature of their shell matrix unaltered resulted in greater *Fucus* recruitment than those in which barnacle tests were heated. Indeed, heating resulted in *Fucus* recruitment patterns similar to cleared control plots. Hence, the *Fucus* recruitment response to barnacle tests can be eliminated by heating the tests. This difference in response by *Fucus* to barnacle tests that differed chemically but were otherwise structurally similar precludes the possibility that the observed *Fucus* recruitment patterns were due to structural characteristics of the substratum associated with to barnacle tests. If structural heterogeneity created by the existence of barnacles was solely responsible for patterns of *Fucus* recruitment, then *Fucus* would have shown similar patterns of recolonization in all of the test only treatments regardless

of the manner in which they were created. Further, had structural influences alone been important, the additional attachment sites inside dead barnacle tests should have resulted in recruitment in the test only treatment exceeding that in the live barnacle treatment. Instead, the observed patterns of *Fucus* recruitment in this study closely mirrored the likely concentration gradient of a chemical cue produced by barnacles in otherwise structurally similar treatments: live barnacles > tests poked > tests torched = cleared control. The chemical has not yet been identified, but it is hypothesized to be arthropodin, the protein settlement factor produced by barnacles to which cyprid larvae respond. Proteins are denatured by heating, and sensitivity to arthropodin would result in highly specific *Fucus* recruitment.

Grazer abundance (e.g. limpets and littorines) was probably reduced in heat-treated quadrats. Though grazers may have subsequently immigrated into the quadrats following heating, grazing intensity was surely reduced compared to the non-heated test only quadrats. Assuming grazers were reduced in the heated test only treatments compared to the poked treatments, and making the further assumption that grazing is important in regulating macroalgal germling success (Burrows & Lodge, 1950; Choat, 1977; J.L. Menge, 1975; Lubchenco & Menge, 1978; Southward & Southward, 1978; Lubchenco, 1980,1983; Hawkins, 1981; Norton & Fetter, 1981; Jernakoff, 1983), a higher level of *Fucus* recruitment should have occurred in the heated treatments compared to the poked treatments. The opposite pattern was observed. Hence, grazing did not regulate *Fucus* germling populations in this study.

To explain the emergence of macro-recruits following times of the year when adult reproductive capability was at a minimum, Ang (1991a) suggested the existence of a 'germling bank' in *Fucus* populations of the northeastern Pacific. He suggested that *Fucus* propagules released during the peak reproductive period may remain viable as germlings at a very small size, and only grow to detectable size (macro-recruits) when physical conditions become favorable. Ang's hypothesis, though experimentally unverified, would explain poor *Fucus* recruitment in the heated treatments because any germlings present would have been killed when the quadrats were established. However, Ang's hypothesis does not account for differences between poked and live barnacle treatments, and the recruitment that did occur on heated tests clearly did not result from a germling bank. Thus, new recruitment, rather than an undemonstrated germling bank of existing plants is the most parsimonious explanation of the observed results.

In barnacle cyprids, which explore a surface thoroughly before choosing a specific site for permanent attachment, the choice of final settlement site seems to be dependent on the strength of adhesion between the molecular surface of the antennulary organ with which the cyprid explores the substrate and the surface itself, rather than through receptor-mediated larval perception (e.g. Crisp, 1984; Rittschof *et al.*, 1984; Gabbott & Larman, 1987; Yule & Walker, 1987; Pawlik, 1992). Crisp (1984) has noted a behavior in which the cyprid tests the tenacity of a potential settlement site by trying to pull its antennulary organs free, much as one would when trying to pull a stuck foot from the mud. Further, Yule and co-workers (Yule & Crisp, 1983; Yule & Walker,1984) have demonstrated the force required to remove a cyprid

attached to a surface treated with settlement factor was significantly greater than for an untreated surface. Additionally, several researchers have noted the "sticky" nature of the barnacle settlement factor proteins (Crisp, 1984; Rittschof & Bonaventura, 1986; Gabbott & Larman, 1987; Pawlik, 1992). Thus, the mechanism of *Fucus* attachment may lie, in part, with the "stickiness" of the proteins that comprise arthropodin.

Given the sticky nature of barnacle settlement-inducing proteins, there seem to be two possible avenues of response of *Fucus* propagules which would explain observed patterns of *Fucus* recruitment. The first is that *Fucus* eggs are able to sense barnacle settlement proteins, and are stimulated to attach directly in response to such a cue. The second potential avenue of *Fucus* response involves an interaction with the non-living compound in which *Fucus* eggs are released. *Fucus* eggs are released from conceptacles of adult plants within a thick mucilage medium (Boney, 1975; Callow *et al.*, 1985; Lobban *et al.*, 1985; personal observation). As *Fucus* eggs appear to have no other means by which to attach to the substratum, the sticky mucus probably facilitates settlement by keeping the eggs in place until they are able to produce an attachment rhizoid that holds the germling in place until a holdfast is formed. If *Fucus* mucus has evolved to adhere more tightly to the sticky settlement factor proteins produced by adult barnacles than other surfaces, then *Fucus* has an effective mechanism for increasing the probability of attachment in sites favorable for survival and growth, as barnacle cover indicates a generally favorable habitat for *Fucus*. Although the laboratory experiments were unsuccessful in demonstrating greater adhesion to extract treated surfaces than to untreated surfaces, the negative

results may have been due to use of whole animal extracts necessitated by the remote field site where the work was conducted. Further laboratory work is required to definitively confirm or reject mucus-arthropodin adhesion strength as a mechanism by which *Fucus* recruits preferentially to live barnacles.

Patterns of *Fucus* recruitment in the field suggest that chemical cues, rather than physical attributes of barnacle cover, are responsible for enhanced *Fucus* recruitment. Although many benthic marine species are able to detect and respond to chemical cues of conspecifics or other species, the *Fucus*-barnacle interaction is of considerable interest because of the evolutionary distance between them.

SUMMARY

Results from field experiments examining the influence of barnacles on recruitment of the common intertidal macroagla, *Fucus gardneri,* indicate that barnacle cover facilitates *Fucus* recruitment. *Fucus* colonization was significantly greater in treatments containing live barnacles than those with empty barnacle tests or in cleared control quadrats. Further, *Fucus* recruitment in empty barnacle test treatments varied with the manner in which barnacles were killed. Quadrats in which barnacles were killed mechanically had greater *Fucus* recruitment than those in which the barnacles were killed by heating, a process which likely denatured surface polypeptides on barnacle tests. These patterns are consistent with the hypothesis that

enhanced recruitment in the presence of barnacles is due to chemical cues produced by barnacles to attract conspecific larvae, rather than due to spatial refuges created by the physical presence of barnacle tests. The mechanism of detection of the chemical cue and response by *Fucus* propagules may be due to molecular adhesion between the "sticky" settlement-inducing proteins produced by barnacles and the mucus in which *Fucus* eggs are released. Although larvae of many marine benthic species have the ability to detect chemical settlement cues, such a response by macroalgal propagules to an animal-produced cue has not been previously reported.

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CHAPTER 7: SUMMARY AND CONCLUSIONS

The population dynamics of selected members of the rocky intertidal community of Kachemak Bay, southcentral Alaska were investigated relative to recruitment and post-recruitment processes, such as predation by the whelk, *Nucella lima*. A major purpose of the study was to determine the importance of recruitment in structuring the community relative to the classical paradigm that community structure is determined by post-recruitment competition and predation. Conducting this research at a location near the northern limit of distribution of many temperate intertidal species provides a major test of the robustness of the classical paradigm because species interactions are likely altered by extremes in the region's physical environment compared to relatively benign temperate latitudes where the paradigm was developed.

The results of the study show that:

- cover of major space-occupying species exhibited high intra-annual variability (seasonality), but was fairly stable over longer time periods
- predation limited the recovery of mussel populations after a severe freeze at some sites, but young barnacle populations were

significantly affected by predation in only one year of three years studied

- barnacle populations were limited by recruitment in the upper intertidal; low intertidal barnacle populations exhibited recruitment rates which usually exceeded the adult saturation point
- recruitment of *Fucus* was significantly enhanced by barnacle cover, and experimental evidence indicates *Fucus* propagules responded to a chemical cue associated with barnacles

Southcentral Alaska experienced a severe freeze in early 1989. Although there were major short-term effects on the rocky intertidal community, the community recovered rapidly. Within 4-5 months, free space resulting from freeze-related mortality was recoionized, primarily by barnacles. The only major successional species replacement that occurred was a shift in dominant cover from barnacles to *Fucus gardneri*. With the exception of mussels, the community achieved relative stability less than two years after the freeze event. These results indicate that the southcentral Alaskan intertidal community was resilient and able to recover quickly from physical perturbations.

The principal manner in which this high-latitude environment affects the intertidal community in Kachemak Bay is through mediation of processes involved in regulating population dynamics. Although biological processes

such as recruitment, predation, and competition can still be important in regulating community structure, the significance of these processes is variable in Kachemak Bay. This variability is a departure from the deterministic nature of community regulatory processes at mid-temperate latitudes.

In Kachemak Bay, barnacle recruitment varied in intensity, both temporally and spatially. Significant inter-annual variations in recruitment occurred, with recruitment in 1992 an order of magnitude greater than in 1991. Barnacle recruitment density was consistently below adult saturation levels in the upper intertidal and above saturation densities in the mid- to low intertidal zone.

Predation also exhibited variable influence in the community. Although both barnacles and mussels were preferred prey of *Nucella*, the impact of predation on these two groups was considerably different. While mussel populations were effectively limited by predation, barnacles were significantly influenced by predation in only one of three years.

An example of the direct impact of winter climatic conditions on interactions affecting community structure is the change in predator impact on mussel populations. The 1989 freeze eliminated large numbers of adult mussels from the community, causing a demographic shift towards younger individuals which were more vulnerable to predation by *Nucella lima.*

Consequently, mussels have not successfully recolonized sites where *Nucella* is present.

During the initial phases of the study, *Fucus gardneri* exhibited little recovery at freeze-impacted sites. After barnacles had become re-established (1-2 years), *Fucus* recruited heavily and eventually dominated cover. The successional observations led to experiments on the relationship between barnacles and *Fucus*. The results indicate that *F. gardneri* germlings attach preferentially to live barnacles due to a heat-labile chemical, possibly a polypeptide associated with the barnacles. Arthropodin is a polypeptide secreted by barnacles as a larval settlement cue. It is possible that *Fucus* propagules are stimulated to attach to barnacles by arthropodin.

Other intertidal algae, particularly kelps, exhibited large seasonal differences in cover. Sub-optimal winter conditions such as short photoperiod, winter storms, and sub-zero air temperatures likely account directly or indirectly for greatly reduced algal cover. In contrast, conditions for plant growth are quite favorable during spring and summer with up to 19 hours of daylight available. The result is a rapid increase in macroalgal cover on the shore with entire stretches of mid- to low intertidal monopolized by algae. The physically-induced seasonal cycles in algal abundance exceed the ability of grazers to control the algal community. The result is a discernible shift in plant community control mechanisms from biological

(grazing pressure) in Washington to physical (environmental conditions) in Alaska (Dethier & Duggins, 1988).

Based upon the population dynamics and species interactions investigated in Kachemak Bay, the mid- to upper intertidal community at high latitudes is structured by recruitment processes. The mid- to low intertidal community appears to function similarly to the classical paradigm of regulation by competition and predation with the major exception that there is high inter-annual variability in the importance of predation relative to recruitment and competition.

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APPENDIX

The enclosed DOS high density diskette contains the raw data used in this dissertation. For information on accessing a particular data set, see the README.TXT located in the main directory.

PLEASE NOTE

The diskette is not included in this material.
It is available for consultation at this author's
graduate school library.

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